



Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi river drainages. Part 1: Serpentes (snakes)

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Abstract.—The herpetofauna of Angola has been neglected for many years, but recent surveys have revealed previously unknown diversity and a consequent increase in the number of species recorded for the country. Most historical surveys focused on the north-eastern and south-western parts of the country, while mostly neglecting the central and south-eastern parts, comprising the provinces of Bié, Moxico, and Cuando Cubango. To address this sampling bias and investigate the conservation importance of the region, a series of rapid biodiversity surveys of the upper Cuito, Cubango, Cuando, Zambezi, and Cuanza river basins were conducted by the National Geographic Okavango Wilderness Project between 2015 and 2019. The first part of those survey results are presented here as an updated checklist of current and historical snake records from the south-eastern region of Angola. In summary, 160 new specimens were collected from the region, comprising 36 species, bringing the total number of recognized snake species for the region to 53. These surveys revealed three new country records (*Amblyodipsas ventrimaculata*, *Crotaphopeltis barotseensis*, and *Dasypeltis confusa*) and led to the description of two novel species in previous publications (*Boaedon branchi* and *B. fradei*), increasing the total number of snake species in Angola to 133. Finally, updated geographic distribution maps are provided for all species encountered in this study for the whole country. This contribution increases our knowledge of this poorly known region of Africa and highlights the need for and importance of similar studies in other undersampled areas.

Keywords. Africa, Cobra, Cuanavale, Cuito, headwater, Okavango Delta, reptile

Resumo—A herpetofauna de Angola foi negligenciada durante muitos anos. A maior parte dos levantamentos realizados a nível histórico incidiram no nordeste e sudoeste do país, sendo o centro e o sudeste, englobando as províncias do Bié, Moxico e Cuando Cubango, menos estudado. Para resolver este enviesamento de amostragem, foram realizados uma série de levantamentos rápidos de biodiversidade das nascentes do alto Cuito, Cubango, Okavango, Cuando, Zambeze e Cuanza pelo National Geographic Okavango Wilderness Project entre 2015 e 2019. Aqui apresentamos a primeira parte dos nossos resultados, uma lista actualizada de registos novos e históricos de cobras do sudeste de Angola. 160 novos registos de espécimes foram documentados na região, incluindo 36 espécies, e elevando o número total de espécies reconhecidas da região para 53. Estes levantamentos revelaram três novos registos para Angola (*Amblyodipsas ventrimaculata*, *Crotaphopeltis barotseensis*, e *Dasypeltis confusa*) e levaram à descrição de duas novas espécies (*Boaedon branchi* e *B. fradei*), aumentando o número de espécies do país para 133. Por fim, produzimos mapas de distribuição atualizados de todas as espécies encontradas neste estudo para todo o território de Angola. Este estudo é uma contribuição significativa para o conhecimento desta região pouco estudada do continente africano, e destaca a necessidade e importância de estudos semelhantes em áreas subamostradas.

Palavras-chave. África, cobra, Cuanavale, Cuito, Delta do Okavango, nascente, réptil

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Introduction

Studies on the historical synthesis of the knowledge on Angolan herpetofauna date back to the 19th century (Bocage 1895), with subsequent updates by Monard (1937a,b). The relatively poor historical documentation of the Angolan herpetofauna is complicated further by the fact that most of the early explorations were restricted to the western regions of the country. Studies in the 20th century, including those of Schmidt (1933, 1936), Parker (1936), Mertens (1938), Bogert (1940), FitzSimons (1959), Hellmich (1957a,b), Poynton and Haacke (1993), Ruas (1996, 2002), and Haacke (2008), did little to correct this geographical bias. The checklists of Laurent (1950, 1954, 1964), Thys van den Audenaerde (1966), and Manaças (1963, 1973, 1982), did however provide some insight into the herpetofauna of north-eastern Angola and its affinity with the Congolian fauna.

Angola experienced one of the most brutal and protracted civil wars after achieving independence from Portugal, which lasted for nearly three decades (1975–2002). In this period, the country's biodiversity was neglected and over-exploited for its natural resources (Huntley and Matos 1992). Following the cessation of hostilities and the ongoing redevelopment of regional infrastructure, the modern biodiversity surveys have begun to focus on poorly surveyed regions of the country in the south-west (Huntley 2009; Ceriaco et al. 2016a; Baptista et al. 2018, 2019a; Butler et al. 2019), north-east (Branch and Conradie 2015; Huntley and Francisco 2015), south-east (Brooks 2012, 2013; Conradie et al. 2016; NGOWP 2017), central (Ceriaco et al. 2014, 2016b, 2018a), and north-west (Ernst et al. 2020) regions. Some of these surveys have targeted areas that had never been scientifically surveyed until recently, leading to the discovery and description of several new species of amphibians (Conradie et al. 2012a, 2013; Ceriaco et al. 2018b, 2021; Nielsen et al. 2020) and reptiles (Conradie et al. 2012b, 2020; Stanley et al. 2016; Branch et al. 2019, 2021; Marques et al. 2019 a,b, 2020; Ceriaco et al. 2020a–c; Hallermann et al. 2020; Lobón-Rovira et al. 2021; Parrinha et al. 2021). Other targeted surveys resulted in the addition of new country records (Branch and Conradie 2013; Conradie and Bourquin 2013; Ernst et al. 2014, 2015; Ceriaco et al. 2014, 2016a; Branch 2018) or resolved previous taxonomic confusion (Channing et al. 2013; Channing and Baptista 2013; Ernst et al. 2015; Marques et al. 2018). Recent synopses of the Angolan herpetofauna include an atlas of all the herpetofauna of Angola (Marques et al. 2018), a checklist of snakes (Branch 2018), and overviews of the reptiles (Branch et al. 2019) and amphibians (Baptista et al. 2019b) of Angola. These works thoroughly present the history of herpetofaunal studies in the country and provide updated checklists for these groups. To date, about 427 herpetofauna species have been recorded within Angolan borders (~293 reptiles and 134 amphibians; Marques

et al. 2018; Baptista et al. 2019b; Branch et al. 2019; Ernst et al. 2020, and the publications with new species descriptions listed above). The documented endemism in Angola is regarded as being relatively low at present (~12% of reptiles and ~15% of amphibians), but it is expected to increase as the knowledge of the country's biodiversity improves.

Subsequent to the reviews of Angolan snakes by Branch (2018) and Marques et al. (2018), four new species have been described for Angola (Conradie et al. 2020; Hallermann et al. 2020), five species have been elevated or resurrected out of synonymy (Branch et al. 2019; Hallermann et al. 2020), and six species were recorded for the first time in the country (Branch 2018; Baptista et al. 2019a; Hallermann et al. 2020; this study); bringing the total number of recognized species of snakes for Angola to 133. Nearly 50% of the Angolan squamate diversity is represented by snakes, of which only nine (6.8%) are regarded as being endemic to the country (Marques et al. 2018; Branch et al. 2019; this study). The Angolan snake richness is just slightly higher than that for South Africa (127 species), a country almost equivalent in size and biome diversity (Branch et al. 2019). The snake richness is higher than in neighboring countries to the east and south (e.g., Botswana 75, Namibia 89, and Zambia 107), but much lower than the more tropical northern countries (e.g., Democratic Republic of the Congo 185 species) (Uetz et al. 2021).

The headwaters of some of southern Africa's major rivers such as the Cubango, Cuito, Cuanavale, and Cuando, which comprise the main Okavango Delta drainage system, are located in the center of the country (Fig. 1). The sources of the Cuanza and Cunene rivers, which drain southward and westward, respectively, into the Atlantic Ocean, as well as major tributaries of the Zambezi River, which drains south and eastward into the Indian Ocean, lie in this same area. For this reason, the area is regarded as the "Heart of Angola." The headwater system of the Okavango Delta drainage system is locally known as "Lisima Lya Mono," which means "Source of Life" and comprises most of the geographic focus of our surveys. This region comprises extensive wetland systems, and has large tracts of intact Miombo woodland, yet it remains one of the most poorly studied regions in Angola, and Africa as a whole. Some of these rivers, namely the Cubango, Cuito, Cuanavale, and Cuando, drain southward into the Okavango Delta system, and provide its main source of water. The Okavango Delta is a major feature in Africa and is a critical water source in the adjacent Kalahari Desert, where animals congregate and create a biodiversity rich region famous for its tourism. While the Okavango Delta is afforded official protected status by Botswana, the Angolan headwaters are not afforded any protected status. Given that the Okavango Delta was identified as a World Heritage Site in 2014 (UNESCO 2014), it is imperative that the delta and its tributaries are conserved to ensure the preservation of

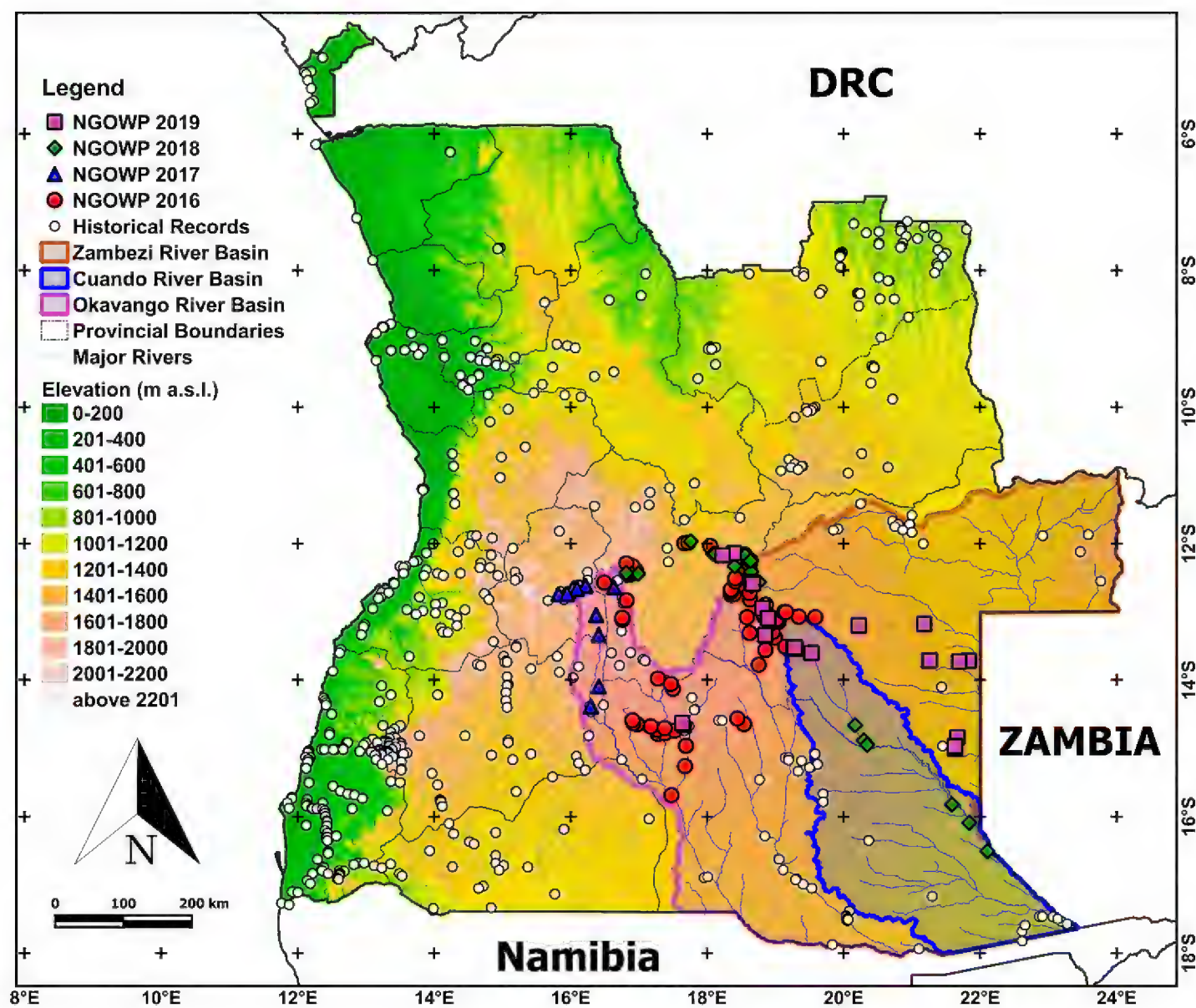


Fig. 1. Map of Angola showing the sampling localities of the National Geographic Okavango Wilderness Project (NGOWP) surveys from 2016 to 2019 and historical herpetofauna records.

this natural wonder. A crucial step for justifying the need to confer protected status on this area is to document its biodiversity.

During the last eight years, the authors and others have been actively documenting the herpetofauna of south-eastern Angola (Brooks 2012, 2013; NGOWP 2015–2019; Conradie et al. 2016). Prior to this, no formal herpetological surveys had been undertaken in south-eastern Angola. Historical material from the region included only opportunistic collections, most of which were confined to the western tributaries of the Cubango River (Bocage 1895; Monard 1931, 1937a,b), with very few records from either the Cuito and Cuando river basins (Angel 1923; Branch and McCartney 1992) or eastern Moxico Province (Laurent 1964; Manaças 1963, 1973).

The aim of this overall study is to document and quantify the herpetofaunal diversity and richness of south-eastern Angola to better understand the conservation importance of this area in regional and national contexts. This paper focuses exclusively on snakes, while similar papers on the sauria (lizards), chelonians (tortoises), and amphibians are currently in preparation.

Materials and Methods

Surveys. This study presents the herpetofauna material and data collected during four main National Geographic Okavango Wilderness Project (NGOWP) expeditions

to south-eastern Angola (2016–2019): (1) two 2016 expeditions to the Cuito, Cuanavale, and Cuando river sources; (2) a 2017 expedition to upper Cubango River; (3) a 2018 expedition to Lungwebungu River; and (4) a 2019 expedition to Mussuma region in eastern Angola (Fig. 1). In addition, updated results from a previous study of south-eastern Angola (Conradie et al. 2016) are included to produce a comprehensive checklist of snakes for the Angolan Okavango-Cuando-Zambezi River drainages.

Study area. The geographical scope of the study area consists of the main Angolan Okavango River Basin (Cuito and Cubango rivers), the Cuando River (and its tributaries), and the Lungwebungu River (tributary of the larger Zambezi River) in south-central and eastern Angola, collectively referred to here as the Angolan Okavango-Cuando-Zambezi River drainages (Fig. 1). *Ad hoc* records from the Cuanza and Cunene rivers are also included in this study, as they contribute to the knowledge of the region. The Cubango River and its tributaries form the western extent of the study area, and are underlain in their headwaters by granite outcrops, characterized in places by rocky substrates, rapids, and waterfalls. In contrast, the Cuito River and its major tributary, the Cuanavale River located in the center of the study area, have wider valleys with water courses that meander across deep Kalahari sands. They are characterized by extensive wet grasslands,

peatlands, and oxbow wetlands (Mendelsohn and Obeid 2004). The impeded drainage and high precipitation in the rainy season cause temporarily waterlogged soils that prevent the development of woodlands along the drainage lines, but support moist grasslands with humic topsoils and dwarf shrubs. These areas act as “sponges” that slowly release water, leading to seasonal flooding in the Okavango Delta towards the end of the rainy season. The Cuando (including its tributary Quembo River) and Lungwebungu rivers have a similar topography to the upper Cuito River, but with west-to-east drainage lines which form a series of floodplains and pans. In the upper reaches of the rivers, the surrounding hills are dominated by various forms of woodland, particularly Miombo woodland (Fig. 2). The core study area surrounding the source lakes is characterised by Angolan Miombo Woodland, while the southern and eastern regions of the rivers are characterised by the drier Zambebian *Baikiaea* woodlands (Burgess et al. 2004). Higher elevation ridges are represented by woodland that is more sparse with scattered proteas and grassland, while the river courses consist of Zambebian flooded grasslands. The elevation varies from 1,850 m above sea level (asl) at the river sources to just below 1,000 m asl in the south and east (Fig. 1), which creates clear north-south and east-west climate gradients. Average rainfall decreases southward, while the average temperature increases (Huntley 2019).

Sampling. Diurnal searches involved active investigation of specific microhabitats, particularly searching beneath rocks and decaying logs, and digging in loose soil or leaf litter. Nocturnal surveys were undertaken around wetlands and the surrounding woodlands with the use of torches. Additionally, all opportunistic visual encounters (e.g., driving between sites) were also recorded. At several base camps during four of the surveys (Table 1), standard Y-shaped intercept drift fence funnel trap arrays were deployed to passively collect specimens. Each Y-shaped trap array consisted of three drift fences (each 10 m long and 50 cm high) radiating from a central pitfall trap, with six two-way funnel traps placed on adjacent sides of each drift fence and three one-way funnels placed at the terminal ends of each drift fence. The trap arrays were installed in varied habitats to ensure the highest possible richness of captured species. Following McDiarmid et al. (2012), the trapping effort was quantified as “trap nights,” where the deployment of a single trap array (comprising a single pitfall, 6 x 2-way and 3 x 1-way funnel traps) for one night was considered to represent one trap night. Snakes retained for subsequent study were humanely euthanized by subcutaneous injection of tricaine methanesulfonate (MS222) solution (Conroy et al. 2009), after which they were formalin-fixed for 48 hours and transferred to alcohol for long-term storage. Prior to formalin fixation, tissue samples (either liver or



Fig. 2. Habitat associated with the different source lakes: (A) Cuito River, (B) Cuanavale River, (C) Quembo River, and (D) Cuando River. *Photos by Kostadin Luchansky.*

Snakes of the Okavango Delta headwater area in Angola

Table 1. Drift fence funnel trap array sites for the 2016–2019 surveys, with brief habitat descriptions, numbers of days installed, and capture rates. R = river. Coordinates are presented in the WGS 84 datum.

Trap site	Latitude (°S)	Longitude (°E)	Elevation (m asl)	Description	Dates	Trap nights	Snakes captured
Cuito R. 1	-12.688693	18.360164	1,426	Marginal vegetation at source lake	15–25 Feb 2016	10	2
Cuito R. 2	-12.688956	18.361870	1,438	Miombo woodland	15–25 Feb 2016	10	0
Cuito R. 3	-12.686020	18.364500	1,414	Grassy south-facing slope with scattered shrubs	16–25 Feb 2016	9	1
Cuanavale R. 1	-13.088937	18.892570	1,360	Marginal grassy vegetation at source lake	27 Feb–15 Mar 2016	18	4
Cuanavale R. 2	-13.092677	18.895518	1,357	Marginal grassy vegetation at source lake	27 Feb–15 Mar 2016	18	5
Cuanavale R. 3	-13.092813	18.894921	1,361	Open Miombo woodland and grass	28 Feb–15 Mar 2016	17	1
Cuanavale R. 4	-13.050780	18.897450	1,396	Sandy basin with scattered grass	29 Feb–15 Mar 2016	15	0
Quembo R. 1	-13.135917	19.044167	1,369	Marginal grassy vegetation at source lake	27 Oct–11 Nov 2016	13	14
Quembo R. 2	-13.135444	19.043972	1,375	Miombo woodland	27 Oct–11 Nov 2016	13	4
Quembo R. 3	-13.130725	19.037245	1,443	Miombo woodland	29 Oct–11 Nov 2016	12	0
Quembo R. 4	-13.135863	19.047088	1,368	Marginal grassy vegetation at source lake	27 Oct–11 Nov 2016	12	10
Cuando R. 1	-13.003929	19.128079	1,351	Marginal grassy vegetation at source lake	12–23 Nov 2016	11	11
Cuando R. 2	-13.004259	19.127187	1,350	Marginal grassy vegetation at source lake	12–23 Nov 2016	11	9
Cuando R. 3	-13.003337	19.135640	1,360	Grassland	13–23 Nov 2016	10	3
Cuando R. 4	-13.001637	19.129598	1,374	Broken Miombo woodland	13–23 Nov 2016	10	1
Lungwebungu R. 1	-12.580126	18.667396	1,298	Miombo woodland	21–25 Apr 2018	4	1
Lungwebungu R. 2	-12.581990	18.665616	1,208	Miombo woodland	21–25 Apr 2018	4	1
Lungwebungu R. 3	-12.580561	18.664190	1,302	Grassland	21–25 Apr 2018	4	0
Lungwebungu R. 4	-12.578694	18.664674	1,305	Grassland	21–25 Apr 2018	4	2
Lower Quembo R. 1	-13.52801	19.28147	1,236	Marginal grassy vegetation next to river	23–29 Nov 2019	7	1
Lower Quembo R. 2	-13.52816	19.28067	1,240	Miombo woodland	23–29 Nov 2019	7	1
Lower Quembo R. 3	-13.52778	19.27455	1,256	Grassland	23–29 Nov 2019	7	0

Table 1 (continued). Drift fence funnel trap array sites for the 2016–2019 surveys, with brief habitat descriptions, numbers of days installed, and capture rates. R = river. Coordinates are presented in the WGS 84 datum.

Trap site	Latitude (°S)	Longitude (°E)	Elevation (m asl)	Description	Dates	Trap nights	Snakes captured
Lower Quembo R. 4	-13.25658	19.27810	1,248	Old cultivated lands	23–29 Nov 2019	7	2
Luanguinga R. 1	-13.70885	21.26234	1,116	Broken Miombo woodland	1–2 Dec 2019	1	0
Lake Hundo 1	-14.99158	21.63096	1,100	Grassland	4–6 Dec 2019	2	1
Lake Hundo 2	-14.97279	21.62890	1,102	Miombo woodland	4–6 Dec 2019	2	0
Lake Hundo 3	-14.97002	21.63139	1,106	Broken Miombo woodland	4–6 Dec 2019	2	0

muscle) were preserved in 96% ethanol for subsequent genetic analysis. Voucher specimens are held in the herpetological collection of Port Elizabeth Museum (PEM) and a representative collection will be returned to the Ministry of Culture, Tourism, and Environment, Luanda, Angola (MCTA, formerly MINAMB).

Specimen identification and morphology. Upon completion of the fieldwork component of the study, preliminary species identifications were made using relevant field guides or published identification keys (Broadley 1983; Branch 1998; Broadley et al. 2003) and through comparison with material housed in the Port Elizabeth Museum. Nomenclature was based on an established online database (The Reptile Database: Uetz et al. 2021) and was updated where needed.

Snout-vent length (SVL, measured from the tip of the snout to the posterior end of the cloacal scale or vent opening) and tail length (TL, measured from the cloacal opening to the tip of the tail) were measured to the nearest 1 mm using a flexible ruler or a tape measure. Size is reported as SVL + TL and truncated tails are indicated by a ‘t’. The following basic scale counts were also documented using a Nikon SMZ1270 binocular stereo microscope: number of longitudinal scale rows (counted one head length behind the head, at midbody, and one head length anterior to the cloacal scale), preoculars, postoculars, temporal scale arrangement, supralabials, supralabials entering orbit, infralabials, infralabials in contact with 1st sublinguals, presence of loreal, ventral scales (following Dowling 1951), subcaudal scales (counted from the posterior edge of the cloaca and excluding the terminal spine), and cloacal scale condition (divided or entire).

Mapping. Geographic distribution maps were produced for all the species of snakes documented during this project for all of their known observation localities within Angola. Data were sourced from published datasets (e.g., Marques et al. 2018), museum databases (e.g., PEM and Ditsong National Museum of Natural History, formerly Transvaal Museum, TM), and online

virtual museum platforms (<http://www.inaturalist.org> and <http://vmus.adu.org.za>). All virtual museum records were checked for diagnostic features to confirm species identifications and only verifiable records were included in the mapping. The online GeoNames gazetteer (<http://www.geonames.org/>) and GEOLocate Web Application (<https://www.geo-locate.org/web/WebGeoref.aspx>) were used to georeference historical records. Distribution data were mapped using QGIS v.3.2 (<http://qgis.org>). We regarded “historical records” as those published in Marques et al. (2018), and all subsequent records were regarded as new.

Results

The surveys documented a total of 160 individual snake records from 78 unique localities in south-eastern Angola, particularly around the source lakes of the Cuito, Cuanavale, Cuando, and Quembo rivers (Fig. 1). Trap arrays deployed for a total of 240 trap nights resulted in the capture of 60 specimens representing 14 species (Table 1), of which seven species were not recorded by other means. A total of 36 snake species (comprising seven families and 23 genera) were recorded during this study (Table 2) and updated species distribution maps in Angola are provided for each of the 36 species (see below). For the mapping exercise, a total of 935 records were collated: 549 historical records from Marques et al. (2018), 118 additional literature records, 35 citizen science platform records, 91 records from other sources (personal photographs, confirmed sightings, and unpublished records of the PEM and TM collections), and 129 records mostly from our surveys. This mapping exercise increased the number of new or previously undocumented records of snakes for Angola by 41.3%.

The following is a checklist of all snake species found during these surveys, including a list of material examined, brief comments on taxonomy, and natural history notes observed when noteworthy. Detailed morphological data and notes on stomach contents and reproduction can be found in Supplementary Table 1 at: <https://doi.org/10.6084/m9.figshare.17057663>. New

Snakes of the Okavango Delta headwater area in Angola

Table 2. Snake species recorded in the Angolan Okavango, Cuando, and Zambezi River basins.

Species	Okavango	Cuando	Zambezi	Source of records
SCOLECOPHIDIA				
Leptotyphlopidae				
<i>Leptotyphlops scutifrons</i> (Peters, 1854)	X			Conradie et al. 2016: 23; Monard 1937: 106
<i>Leptotyphlops kafubi</i> (Boulenger, 1919)			X	This study; Laurent 1964: 91
<i>Namibiana rostrata</i> (Bocage, 1886)	X			This study
Typhlopidae				
<i>Afrotiphlops angolensis</i> (Bocage, 1866)			X	This study; Manaças 1973: 189
<i>Afrotiphlops anomalus</i> (Bocage, 1873)	X			Monard 1937: 103
<i>Afrotiphlops schmidtii</i> (Laurent, 1956)			X	This study; Laurent 1964: 89
PYTHONOIDEA				
Pythonidae				
<i>Python natalensis</i> Smith, 1840	X	X	X	This study; Conradie et al. 2016: 23; Monard 1937: 108
COLUBROIDEA				
Colubridae				
<i>Crotaphopeltis barotseensis</i> Broadley, 1968	X	X		This study
<i>Crotaphopeltis hotamboeia</i> (Laurenti, 1768)	X		X	This study; Conradie et al. 2016: 19; Branch and McCartney 1992: 2; Laurent 1964: 110; Monard 1937: 129
<i>Dasypeltis confusa</i> Trape and Mané, 2006	X		X	This study
<i>Dasypeltis scabra</i> (Linnaeus, 1758)	X		X	Manaças 1973: 192; Monard 1937: 114
<i>Dipsadoboa shrevei</i> (Loveridge, 1932)			X	Laurent 1964: 110
<i>Dispholidus typus punctatus</i> Laurent, 1955			X	Laurent 1964: 114; Manaças 1973: 193
<i>Dispholidus typus viridis</i> (Smith, 1828)	X	X		This study; Branch and McCartney 1992: 2
<i>Philothamnus angolensis</i> Bocage, 1882	X		X	This study; Monard 1937: 121; Manaças 1973: 191
<i>Philothamnus heterolepidotus</i> (Günther, 1863)	X	X	X	This study; Conradie et al. 2016: 19; Manaças 1973: 191; Laurent 1964: 105
<i>Philothamnus hoplogaster</i> (Günther, 1863)			X	This study
<i>Philothamnus semivariatus</i> (Smith, 1840)	X	X	X	This study; Laurent 1964: 107; Monard 1937: 114
<i>Philothamnus ornatus</i> (Bocage, 1872)	X	X		This study; Conradie et al. 2016: 19; Monard 1937: 114
<i>Thelotornis capensis oatesi</i> (Günther, 1881)	X			This study; Conradie et al. 2016: 19; Monard 1937: 128
Natricidae				
<i>Limnophis bangweolicus</i> (Mertens, 1936)		X	X	Conradie et al. 2020: 16; Conradie et al. 2016: 22; Laurent 1964: 100
<i>Limnophis bicolor</i> (Günther, 1865)	X	X	X	This study; Conradie et al. 2020: 14

Table 2 (continued). Snake species recorded in the Angolan Okavango, Cuando, and Zambezi River basins.

Species	Okavango	Cuando	Zambezi	Source of records
<i>Natriciteres olivacea</i> (Peters, 1854)		X	X	This study; Conradie et al. 2016: 22
ELAPSOIDEA				
Atractaspididae				
<i>Atractaspis congica</i> Peters, 1877			X	Laurent 1964: 122
Aparallactidae				
<i>Amblyodipsas polylepis polylepis</i> (Bocage, 1873)	X			This study
<i>Amblyodipsas ventrimaculata</i> (Roux, 1907)	X			This study
<i>Aparallactus capensis</i> Smith, 1849	X			Branch and McCartney 1992: 2
<i>Xenocalamus mechowii</i> Peters, 1881	X	X	X	This study; Branch and McCartney 1992: 2
Lamprophiidae				
<i>Boaedon angolensis</i> Bocage, 1895	X			This study
<i>Boaedon branchi</i> Hallermann, Ceriaco, Schmitz, Ernst, Conradie, Verburgt, Marques, and Bauer, 2020	X			This study; Conradie et al. 2016: 22
<i>Boaedon fradei</i> Hallermann, Ceriaco, Schmitz, Ernst, Conradie, Verburgt, Marques, and Bauer, 2020		X	X	This study; Conradie et al. 2016: 22
<i>Limaformosa capensis</i> (Smith, 1847)	X		X	Laurent 1964: 94; Branch and McCartney 1992: 2
<i>Lycophidion multimaculatum</i> Boettger, 1888	X	X		This study; Branch and McCartney 1992: 1
Prosymnidae				
<i>Prosymna ambigua ambigua</i> (Bocage, 1873)	X			Monard 1937: 114
<i>Prosymna angolensis</i> Boulenger, 1915	X	X		This study
Psammophiidae				
<i>Kladirostratus acutus</i> (Günther, 1888)	X	X	X	This study; Manaças 1973: 194
<i>Psammophis angolensis</i> (Bocage, 1872)			X	Laurent 1964: 114
<i>Psammophis jallae</i> Peracca, 1896	X	X		This study; Angel 1922: 116
<i>Psammophis mossambicus</i> Peters, 1882	X	X	X	This study; Conradie et al. 2016: 22; Branch and McCartney 1992: 2; Manaças 1973: 191; Laurent 1964: 113; Monard 1937: 128
<i>Psammophis zambiensis</i> Hughes and Wade, 2002	X	X	X	This study
<i>Psammophis subtaeniatus</i> Peters, 1882	X	X	X	Conradie et al. 2016: 22
<i>Psammophylax tritaeniatus</i> (Günther, 1868)	X		X	Laurent 1964: 110
Pseudaspidae				
<i>Pseudaspis cana</i> (Linnaeus, 1758)	X			Monard 1937: 113
Elapidae				
<i>Dendroaspis polylepis</i> Günther, 1864	X	X		This study; Conradie et al. 2016: 22

Snakes of the Okavango Delta headwater area in Angola

Table 2 (continued). Snake species recorded in the Angolan Okavango, Cuando, and Zambezi River basins.

Species	Okavango	Cuando	Zambezi	Source of records
<i>Elapsoidea guentherii</i> Bocage, 1866			X	Laurent 1964: 117
<i>Elapsoidea semiannulata semiannulata</i> Bocage, 1882	X		X	This study; Manaças 1981: 23
<i>Naja (Uraeus) anchietae</i> (Bocage, 1879)	X			Monard 1937: 136
<i>Naja (Afronaja) mossambica</i> (Peters, 1854)	X			Conradie et al. 2016: 22
<i>Naja (Afronaja) nigricollis</i> Reinhardt, 1843	X			This study; Monard 1937: 136
Viperidae				
<i>Bitis (Bitis) arietans</i> (Merrem, 1820)	X		X	This study; Branch and McCartney 1992: 2; Conradie et al. 2016: 23; Monard 1937: 141
<i>Bitis (Macrocerastes) gabonica</i> (Duméril, Bibron, and Duméril, 1854)			X	This study; Laurent 1964: 128
<i>Causus bilineatus</i> (Boulenger, 1905)	X	X	X	This study; Laurent 1964: 125
<i>Causus rhombeatus</i> (Lichtenstein, 1823)	X	X		This study; Conradie et al. 2016: 23; Laurent 1964: 123; Manaças 1973: 197; Monard 1937: 141
Species totals: 53	40	20	27	

distributional data used to compile the distribution maps can be found in Supplementary Table 2 at: <https://doi.org/10.6084/m9.figshare.17057678>. Two abbreviations used in these listings are: asl – above sea level, and DOR – dead on road. This checklist follows the higher-level taxonomic classification suggested by Zaher et al. (2019).

Superfamily: Typhlopoidea

Family: Leptotyphlopidae

Leptotyphlops kafubi (Boulenger, 1919)

Shaba Thread Snake (Fig. 3, Map 1)

Material: PEM R27372, Camp at tributary (Luandai River) of the Luanguinga River, Moxico Province, -13.70885° 21.26234°, 1,116 m asl. **Description:** Midbody scale rows 14; 223 middorsal scales; 21 subcaudals, 10 scales around tail; supraoculars separated from the rostral by a discrete prefrontal; anterior supralabial present; cloacal scale is heart-shaped. Size: 128 + 12 mm. **Habitat and natural history notes:** Collected in Miombo woodland. **Comments:** The new specimen is only the third record for the country. Laurent (1964) assigned two specimens from Moxico Province (Calundo and ‘Chutes de la Luisavo, Cabinda, Haut Zambeze’) to *Leptotyphlops emini emini* (Boulenger, 1890). Later, Broadley and Watson (1976) re-assigned this material to *Leptotyphlops nigricans nigricans* (Schelgel, 1839), but Broadley and Broadley (1999) subsequently transferred it to *Leptotyphlops kafubi*. Leptotyphlopoid snakes show deep genetic divergences and comprise numerous cryptic taxa that still await formal description (Adalsteinsson et al. 2009; Busschau et al. 2021). Cryptic

diversity is expected among Angolan Leptotyphlopidae and warrants further studies.

Namibiana rostrata (Bocage, 1886)

Angolan Beaked Thread Snake (Fig. 4, Map 2)

Material: PEM R23261, Cuchi Gorge, Cuando Cubango Province, -14.59000° 16.90758°, 1,350 m asl. **Description:** Midbody scale rows 15; 245 middorsal scales; 20 subcaudals, 12 scales around tail; supraoculars present; rostral fused with prefrontal; beak hooked; anterior supralabial present; cloacal scale heart-shaped. Size: 132 + 9 mm. **Habitat and natural history notes:** A single specimen was collected from the Cuchi River, a tributary of the Cubango River, under a rock in Miombo woodland. **Comment:** This is an Angolan endemic, restricted to southern Angola (Branch 2018). The new record represents the eastern-most locality for this species and the first record for the larger Okavango Delta system. This species was recently recorded from Bicular National Park and surroundings (Baptista et al. 2019a; Butler et al. 2019).

Family: Typhlopidae

Afrotiphlops angolensis (Bocage, 1866)

Angolan Blind Snake (Fig. 5, Map 3)

Material: PEM R23357, en route to Cuito River source, Moxico Province, -12.43405° 18.43603°, 1,533 m asl. **Description:** Midbody scale rows 23; 318 ventral scales; 11 subcaudals. Size: 215 + 3.6 mm. **Habitat and natural history notes:** A single specimen was collected when a fallen tree obstructing the road was



Fig. 3. *Leptotyphlops kafubi* from the camp at a tributary (Luandai River) of the Luanguinga River. Photo by Werner Conradie.

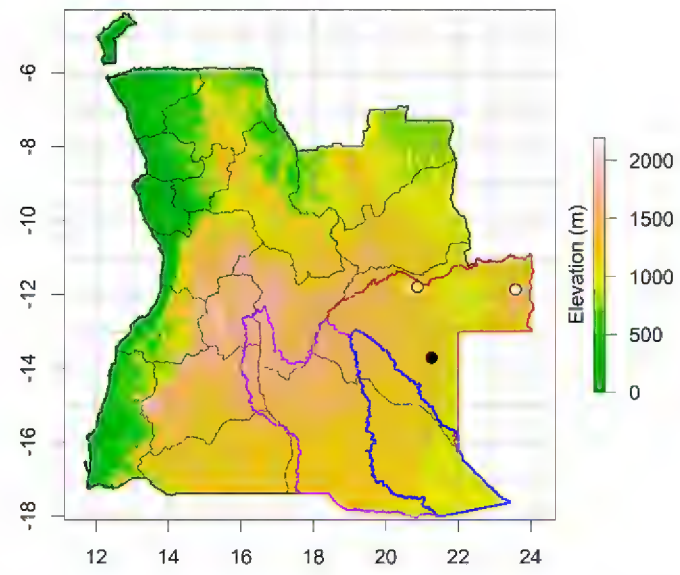


Fig. 4. *Namibiana rostrata* from Cuchi River Gorge. Photo by Werner Conradie.

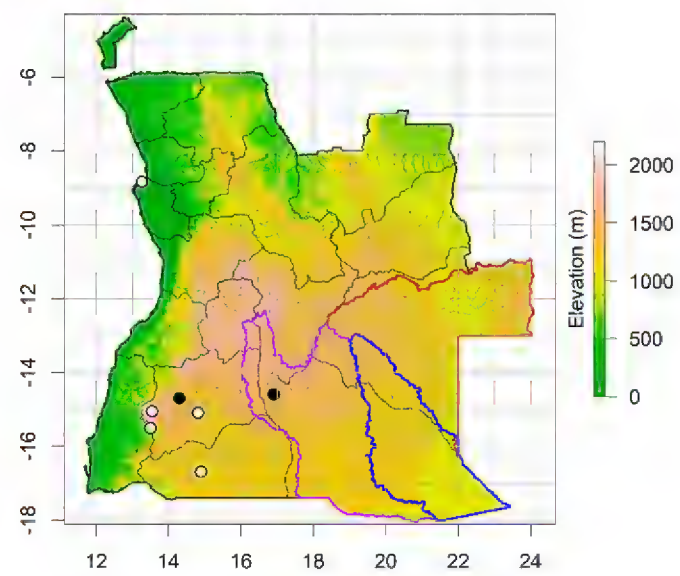


Fig. 5. *Afrottyphlops angolensis* en route to Cuito River source. Photo by Werner Conradie.

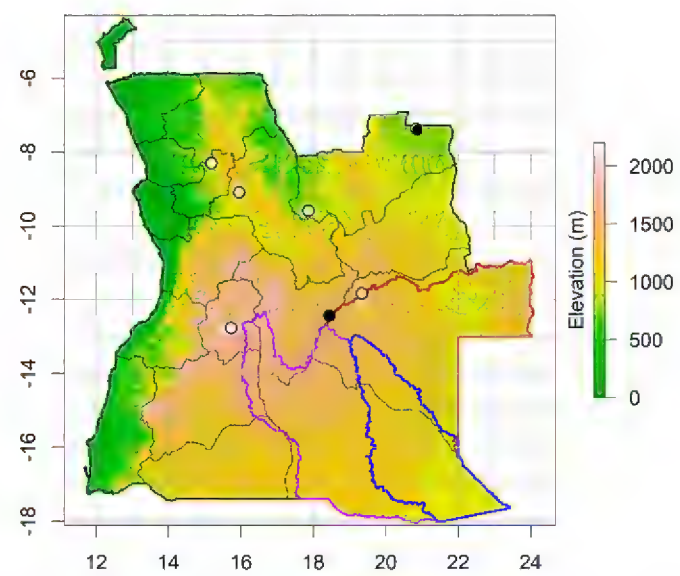
removed in pristine Miombo woodland. **Comment:** The specimen was identified as *A. angolensis* using the key provided by Broadley and Wallach (2009), but this needs to be confirmed using genetic data. This species was originally described from Angola by Bocage (1866) but is represented by fewer than 10 records from the country (Marques et al. 2018). Outside of Angola, it is widespread



Map 1. Distribution of *Leptotyphlops kafubi* in Angola. Historical records are indicated by white dots while all new records are indicated by black dots. Axis values are in degrees (°).



Map 2. Distribution of *Namibiana rostrata* in Angola.



Map 3. Distribution of *Afrottyphlops angolensis* in Angola.

throughout much of the Democratic Republic of the Congo (DRC) through to Uganda, Kenya, Tanzania, and Zambia (Broadley and Wallach 2009). Many historical names are currently subsumed under this name (Broadley and Wallach 2009), and given its large geographical range, there is a need to investigate this species complex in a phylogenetic framework.



Fig. 6. *Afrotrophlops schmidti* from Lungwebungu River. Photo by Werner Conradie.

Afrotrophlops schmidti (Laurent, 1956)

Schmidt's Blind Snake (Fig. 6, Map 4)

Material: PEM R23993, en route to Lungwebungu River, Moxico Province, -12.44190° 18.62826° , 1,419 m asl; PEM R23979, Lungwebungu River, -12.58131° 18.66378° , 1,298 m asl. **Description:** Midbody scale rows 22 and 24; 347 and 336 ventral scales; 9 and 10 subcaudals. Largest specimen: 435 + 5.9 mm. **Habitat and natural history notes:** Two specimens were collected in Miombo woodland, both actively moving in the early morning. **Comment:** One of these specimens was featured in Branch (2018), but under the incorrect name *A. mucruso*. Re-examination of the material confirms it to be assignable to *A. schmidti* based on the key provided by Broadley and Wallach (2009). Broadley and Wallach (2009) discussed the complex taxonomic history of the species. Broadley et al. (2003) mention that material from western Zambia and the DRC, including the holotype from Katanga, are blotched, similar to our material. The only other material for Angola is from the eastern part of the country (Calundo and Cazombo: Laurent 1964).

Superfamily: Pythonoidea

Family: Pythonidae

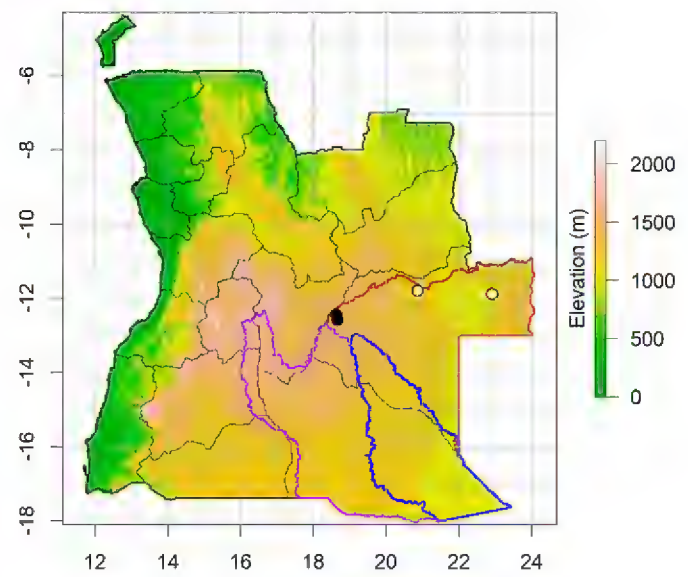
Python natalensis Smith, 1840

Southern Rock Python (Map 5)

Material: Quembo River, -13.48626° 19.24775° , 1,243 m asl (sighting only); Quembo River, -13.93008° 19.41776° , 1,198 m asl (sighting only); Cuando River, -13.46214° 19.54561° , 1,229 m asl (sighting only); 10 km south of Cuanavale River source, approx. -13.17192° 18.85896° , 1,544 m asl (sighting only).

Additional photographic record: Cuatir, Cuando Cubango Province, -16.48523° 18.20304° , Stefan van Wyk. **Habitat and natural history notes:** Specimens were sighted sunning themselves next to main rivers.

Comments: Three species of pythons are known from Angola (*P. anchietae*, *P. sebae*, and *P. natalensis*; Branch 2018; Marques et al. 2018). We assigned our material



Map 4. Distribution of *Afrotrophlops schmidti* in Angola.

to *P. natalensis* based on head coloration and scalation (Broadley 1984, 1999). This species is widespread south of -10° latitude, approximately the latitude of the lower Cuanza River in Angola. This is the largest snake species occurring in the study area, but it was seldom encountered. Although it is considered as a protected species in Angola (Decreto Executivo No. 201/16, 26 de Abril de 2016), we observed a python being cooked in a hunter's camp, 10 km south of the Cuanavale River source (Chris Boyes, pers. comm.). Pythons are often found in the local Angolan markets or sold on the side of the road in the form of live animals, fresh meat, smoked meat, and leather products (Marques et al. 2018; Gonçalves et al. 2019).

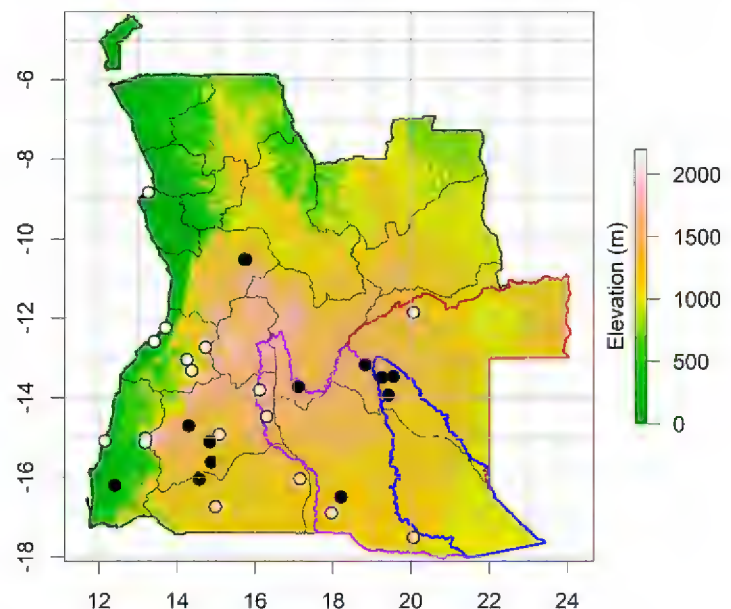
Superfamily: Colubroidea

Family: Colubridae

Crotaphopeltis barotseensis Broadley, 1968

Barotse Water Snake (Fig. 7, Map 6)

Material: PEM R23271, Cuanavale River source, Moxico Province, -13.09033° 18.89396° , 1,356 m asl; PEM R23348, small tributary source lake 6 km SE of Cuito River source, Moxico Province, -12.73675° 18.39310° , 1,446 m asl; PEM R23323, Cuito River Source Lake, Moxico Province, -12.68935° 18.36012° ,



Map 5. Distribution of *Python natalensis* in Angola.

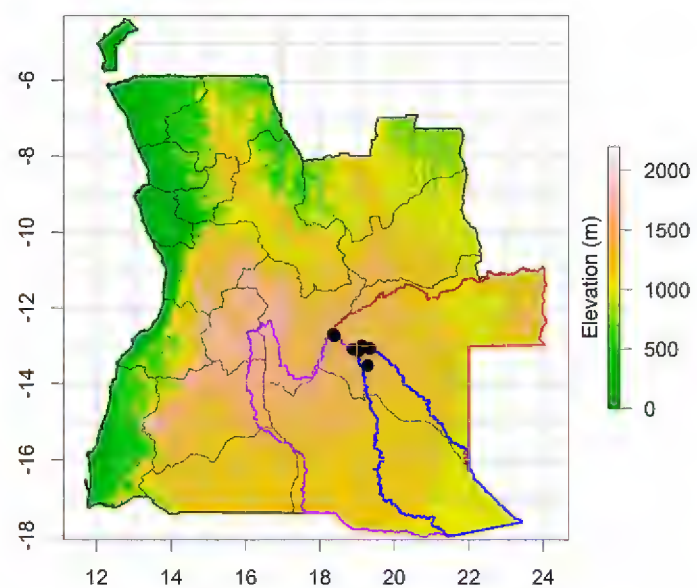


Fig. 7. *Crotaphopeltis barotseensis* from Cuando River source. Photo by Werner Conradie.

1,435 m asl; PEM R23466, Quembo River source, Moxico Province, -13.13592° 19.04417° , 1,369 m asl; PEM R23406, dammed tributary of Cuando River, Moxico Province, -13.06838° 19.34366° , 1,287 m asl; PEM R23439, Cuando River Source, Moxico Province, -13.00393° 19.12808° , 1,351 m asl; PEM R27360, Quembo River right tributary (Micongo River) past village, Moxico Province, -13.51877° 19.28487° , 1,248 m asl. **Description:** Dorsal scales smooth and in 17 rows at midbody; 151–168 ventrals; 29–42 paired subcaudals; 1 preocular; 2 postoculars; 1+2 temporals; 8 supralabials, the 3rd–5th entering the orbit; 10 infralabials, the first five in contact with the anterior chin shield; cloacal scale entire. Largest female: 279 + 37 mm (PEM R23348); largest male: 407 + 47 mm (PEM R27360). **Habitat and natural history notes:** All specimens were found in grassland associated with large water sources. One specimen had an unidentified *Ptychadena* in its stomach, while another had frog eggs (possibly *Hyperolius*) in its stomach. **Comment:** These are the first records of this aquatic snake for Angola. Although some minor morphological differences were observed among the newly collected Angolan material, the specimens agree with those observed by Rasmussen (1997). The new material increases the maximum number of ventral scales and provides both the lowest and highest subcaudal scale



Fig. 8. *Crotaphopeltis hotamboeia* from west of Menongue. Photo by Luke Verburgt.



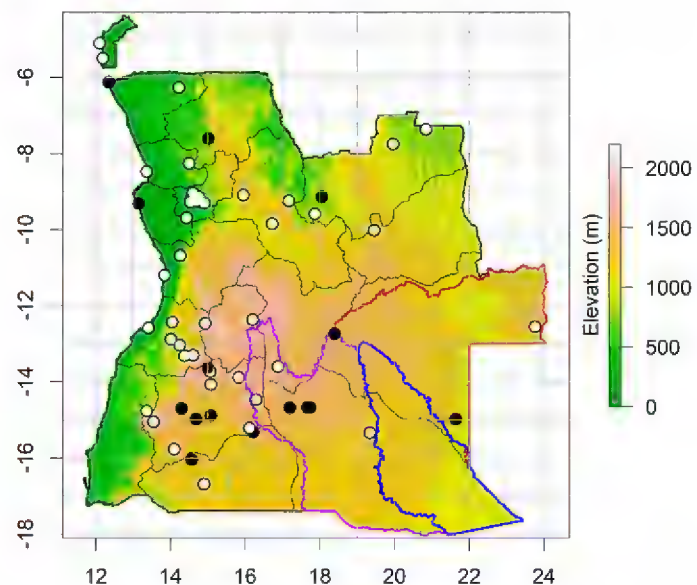
Map 6. Distribution of *Crotaphopeltis barotseensis* in Angola.

counts. The holotype is unique in that the upper postocular is excluded from the supraocular by the parietal, while in all the new material the upper postocular is in broad contact with the supraocular. Our collection has already been included in the previous checklist of Angolan snakes (Branch 2018) and the recent Angolan biodiversity book (Branch et al. 2019). The closest previous record is the type specimen from Kalabo in Zambia (~450 km to the east; Broadley 1968). This material has also been used in a recent phylogenetic study of the genus and *C. barotseensis* was recovered as the sister lineage to all other *Crotaphopeltis* (Engelbrecht et al. 2019).

Crotaphopeltis hotamboeia (Laurenti, 1768)

White-lipped Snake (Fig. 8, Map 7)

Material: PEM R23301, HALO Menongue, Cuando Cubango Province, -14.66317° 17.66521° , 1,372 m asl; PEM R23349–50, small tributary source lake 6 km SE of Cuito River source, Moxico Province, -12.73675° 18.39310° , 1,446 m asl; PEM R23532, EN280 West of Menongue, Cuando Cubango Province, -14.67908° 17.19325° , 1,415 m asl; PEM R27361–9, INBAC: WC-7063, Lake Hundo, Moxico Province, -14.97431° 21.62966° , 1,100 m asl. **Description:** Dorsal scales smooth anteriorly and weakly keeled posteriorly, and in 19 rows at midbody; 139–158 ventrals; 31–41 paired



Map 7. Distribution of *Crotaphopeltis hotamboeia* in Angola.



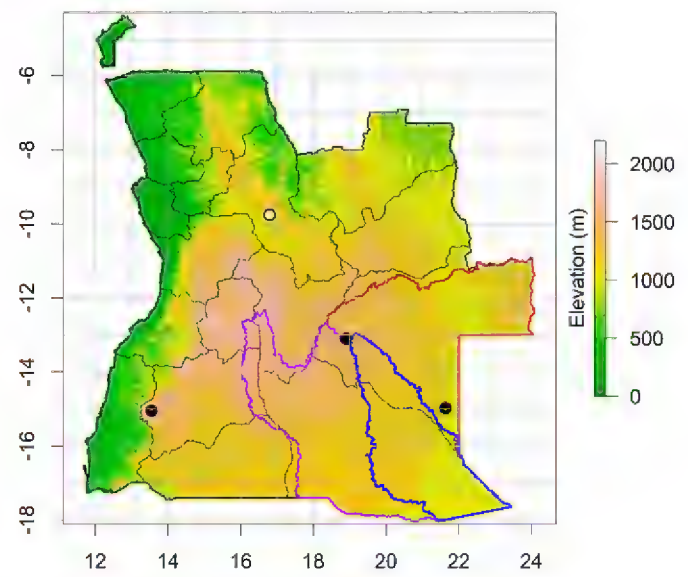
Fig. 9. *Dasypeltis confusa* from Cuito River source. Photo by Werner Conradie.

subcaudals; 1 preocular; 2 postoculars; temporals 1+2; 8 supralabials, the 3rd–5th entering the orbit; 10 infralabials, first five in contact with the anterior chin shield; cloacal scale entire. Largest female: 465 + 66 mm (PEM R27361); largest male: 485 + 76 mm (PEM R23532). **Habitat and natural history notes:** Specimens were found in grassland associated with large water sources, and these populations lack the red/orange lip coloration typical of snakes found further south. Five specimens had frogs (*Hyperolius angolensis* or *Kassina senegalensis*) in their stomachs. **Comment:** A common and widespread species in Angola (Marques et al. 2018). Surprisingly, a recent study showed only shallow genetic divergences among *C. hotamboeia* across its range (Engelbrecht et al. 2019).

Dasypeltis confusa Trape and Mané, 2006

Confusing Egg Eater (Fig. 9, Map 8)

Material: PEM R23272, Cuanavale River source, Moxico Province, -13.09033° 18.89396°, 1,356 m asl; PEM R27745, Lake Hundo, Moxico Province, -14.9700° 21.6314°, 1,106 m asl. **Description:** Dorsal scales strongly keeled and in 25 and 26 rows at midbody; 196 and 209 ventrals; 63 paired subcaudals; 1 preocular; 2 postoculars; 2 temporals; 7 supralabials, with 3rd–5th entering the orbit; 7 and 8 infralabials, with first three in contact with the anterior chin shield; cloacal scale entire. Largest male: 396 + 78 mm (PEM R27745). **Habitat and natural history notes:** PEM R23272 exhibited the typical threat display by rubbing its scales and opening its mouth to show the black interior (<https://www.facebook.com/pemherp/videos/1083042281853751/>). **Comment:** A new lower range for the number of ventral scales is provided. Records of *Dasypeltis* spp. are known from all over Angola, from western to central and eastern Angola (Marques et al. 2018), but species identification to date has been confused. This widespread distribution includes a range of habitats, such as coastal floodplains and the central plateau. Unpublished barcoding results of the Cuanavale River source specimen confirms the identification of the species as *D. confusa*. This



Map 8. Distribution of *Dasypeltis confusa* in Angola.

represents the first genetically confirmed record of this recently described species for Angola. Other material from Cangandala (Ceriaco et al. 2016b, as *D. scabra*; see Branch 2018) and from the Humpata Plateau (PEM R22056; field number NB0738; Baptista et al. 2018) can be assigned to this species as they all exhibit the typical ‘5L’ color pattern (Gans 1959; Trape and Mané 2006). We also tentatively assign an unpatterend reddish-orange specimen photographed (Fig. 10) at the Cuando River to this species.

Dispholidus typus viridis (Smith, 1828)

Boomsnang (Fig. 11, Map 9)

Material: PEM R23346, Village Fio, 30 km north of Menongue (DOR), Cuando Cubango Province, -14.05786° 17.46992°, 1,445 m asl; PEM R23542, EN140 north of Menongue (DOR), Cuando Cubango Province, -14.05786° 17.46992°, ~1,504 m asl; PEM R23519, Quembo River source, Moxico Province, -13.11452° 19.02469°, 1,512 m asl. **Description:** Dorsal scales elongated and keeled, in 18–19 rows at midbody; 174–186 ventrals; 116 paired subcaudals; 1 preocular; 2 postoculars; temporals 1+2; 7 supralabials, with 3rd and 4th entering the orbit; 10 infralabials, the first five



Fig. 10. *Dasypeltis* cf. *confusa* from Cuando River. Photo by Götz Neef.



Fig. 11. Juvenile *Dispholidus typus viridis* from Quembo River source. Photo by Werner Conradie.

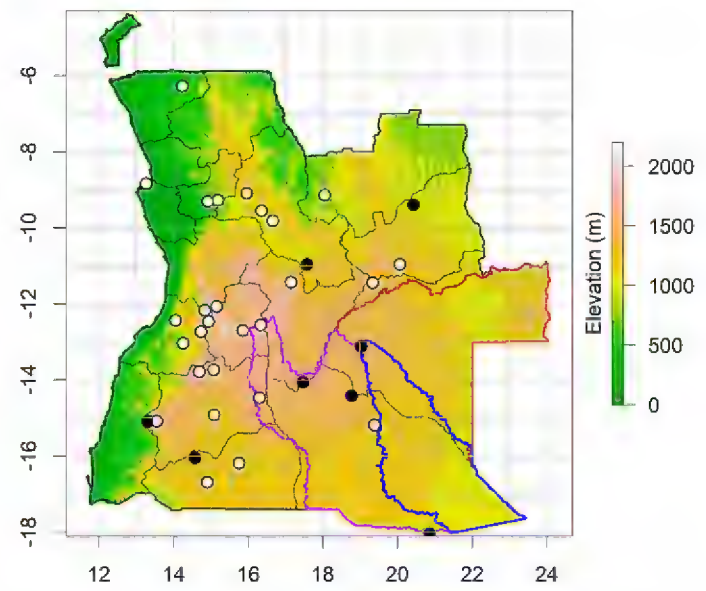
in contact with the anterior chin shield; cloacal scale divided. Largest female: 804 + 228 mm (PEM R23346); largest male: 233 + 89 mm (PEM R23519). **Habitat and natural history notes:** Juvenile specimen found in mature Miombo. **Comment:** This is a common and widespread venomous species of snake throughout most of Africa, and comprises numerous forms (*D. t. typus*, *D. t. viridis*, *D. t. punctatus*, and *D. t. kivuensis*). The Angolan material is often restricted to two subspecies, *D. t. punctatus* (mostly northern Angola) and *D. t. viridis* (mostly southern and central Angola; see Marques et al. 2018; Baptista et al. 2019a). The elevation of these two forms to full species was proposed in the unpublished thesis by Eimermacher (2012), but awaits formal publication. The new material can be assigned to *D. t. viridis* based on uniform coloration and higher subcaudal scale counts.

Philothamnus angolensis Bocage, 1882
Angolan Green Snake (Fig. 12, Map 10)

Material: PEM R23518, 33 km W of Menongue, Cuelel River, Cuando Cubango Province, -14.70511° 17.38014°, 1,500 m asl; PEM R23263, Cuchi Gorge, Cuando Cubango Province, -14.59000° 16.90758°, 1,350 m asl. **Description:** Dorsal scales smooth and in 15 rows at midbody; 132–175 ventrals; 88–103

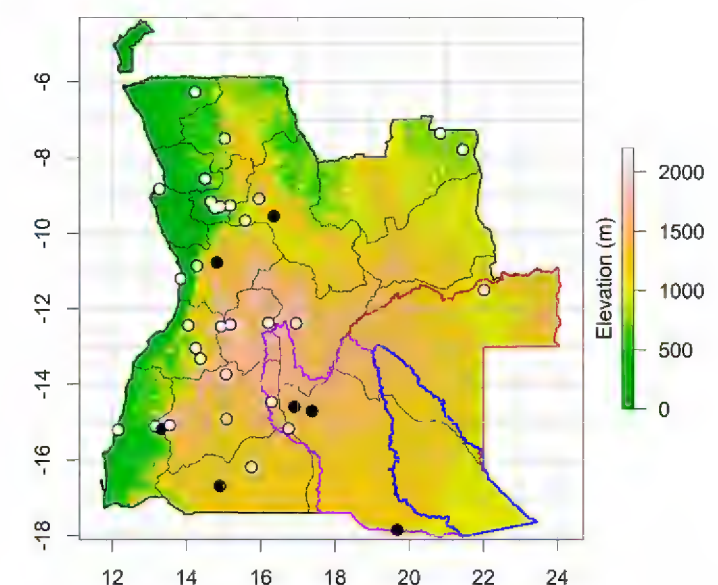


Fig. 12. *Philothamnus angolensis* from Cuelel River, west of Menongue. Photo by Luke Verburgt.



Map 9. Distribution of *Dispholidus typus viridis* in Angola.

paired subcaudals; weak posterior ventral keeling; 1 preocular; 2 postoculars; temporals 1+1; 9 supralabials, with 4th–6th entering the orbit; 10 infralabials, with first five in contact with the anterior chin shield; cloacal scale divided. Largest female: 588 + 262 mm (PEM R23518); largest male: 290 + 130 mm (PEM R23392). **Habitat and natural history notes:** All specimens were collected from the Cubango River and its tributaries to the west of the study area, which is dominated by rockier substrate and dry Miombo woodland. **Comment:** First described from Capangombe in Angola as *Philothamnus angolensis* (Bocage 1882), but later considered to be part of *Philothamnus irregularis* by most authors, including Bocage himself (Bocage 1895; Parker 1936; Monard 1937b; Bogert 1940; Hellmich 1957b; Laurent 1964). Hughes (1985) resolved the taxonomic confusion by restricting *P. irregularis* to West Africa and reinstating *P. angolensis* for the southern and eastern populations. Many of the historical records from Angola referred to as *P. irregularis* are now assignable to either *P. angolensis* or *P. hoplogaster*. *Philothamnus angolensis* is widespread across most of southern, central, and eastern Africa (Branch 1998; Spawls et al. 2018). Within Angola, the species is known mostly from central and western Angola, with isolated records in the north-east (Marques et al. 2018). Although no records are known



Map 10. Distribution of *Philothamnus angolensis* in Angola.



Fig. 13. *Philothamnus heterolepidotus* from Cuanavale River source. Photo by Werner Conradie.

from south-eastern Angola, there are records from the Okavango Delta in Botswana and the Zambezi Region (= Caprivi Strip) in Namibia (Auerbach 1987; Broadley and Blaylock 2013), and thus the presence of this species is expected in south-eastern Angola. A recent virtual museum record (ReptileMap 166590) from the Angolan side of the Cubango River, just west of Calai, fills the gap between the southern Angolan and Namibian records.

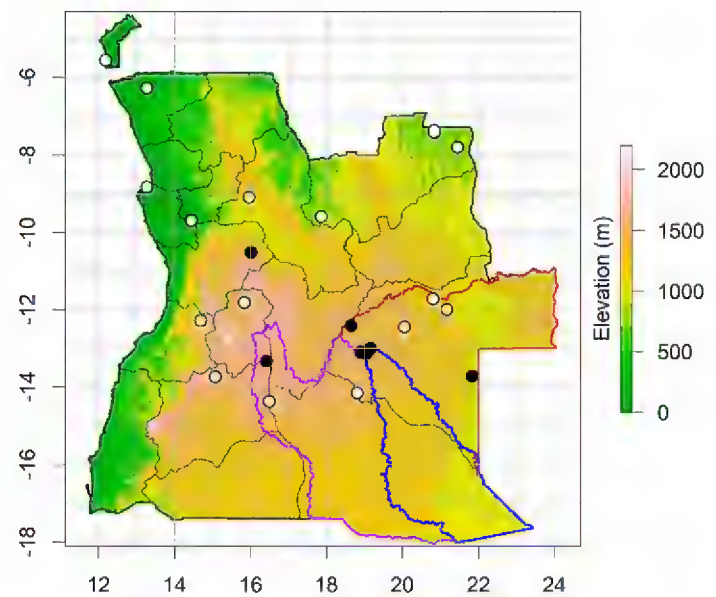
Philothamnus heterolepidotus (Günther, 1863)

Slender Green Snake (Fig. 13, Map 11)

Material: PEM R23281–3, Cuanavale River source lake, Moxico, -13.09330° 18.89396°, 1,356 m asl; PEM R27374, INBAC: WC-7094, Luvu River camp, Moxico, -13.71200° 21.83538°, 1,082 m asl; PEM R23470–4, INBAC: WC-4619, Quembo River Source, Moxico, -13.13592° 19.04417°, 1,369 m asl; PEM R23413, road east of Cuando River Source, Moxico, -13.00118° 19.15739°, 1,335 m asl. **Description:** Dorsal scales smooth and in 15 rows at midbody; 171–186 angular ventrals; 110–130 paired smooth subcaudals; 1 preocular; 2 postoculars; temporals 1+1; 9 supralabials, the 4th–6th entering the orbit; 10 infralabials, the first five in contact with the anterior chin shield; cloacal scale divided. Largest female: 529 + 249 mm (PEM R23474); largest male: 520 + 270 mm (PEM R23283). **Habitat and natural history**



Fig. 14. *Philothamnus hoplogaster* from Luvu River. Photo by Werner Conradie.



Map 11. Distribution of *Philothamnus heterolepidotus* in Angola.

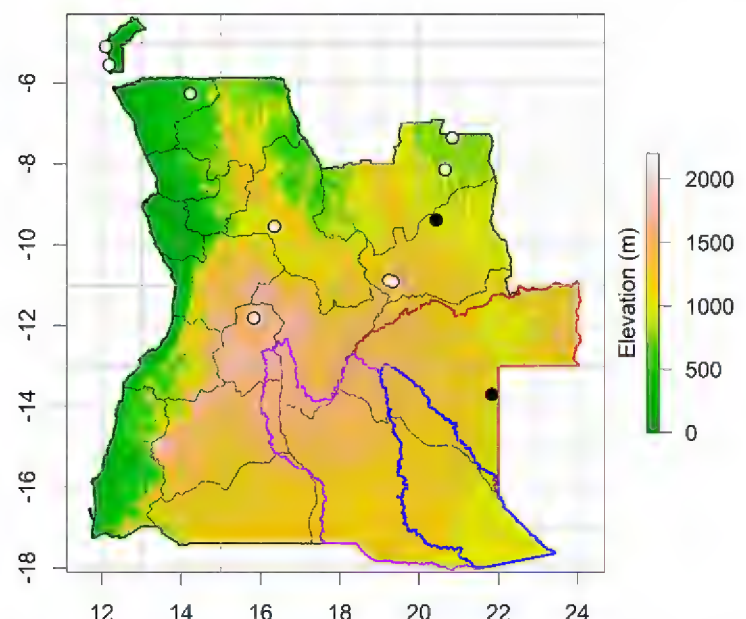
notes: Commonly found and trapped near water sources. Three specimens had reed frogs (*Hyperolius* sp.) in their stomachs. One female (PEM R23472) had four eggs, largest measuring 29.0 x 7.8 mm. A few individuals were captured at night while sleeping in trees near the water.

Comment: In the literature, *P. heterolepidotus* is recorded to have either smooth or angular ventral scales (Broadley et al. 2003; Spawls et al. 2018; Chippaux and Jackson 2019). All of the new material presented here exhibited weakly developed angular ventral scales. The species is known from a number of localities in Angola (Marques et al. 2018). The record referred to as *P. hoplogaster* in Conradie et al. (2016) is actually a *P. heterolepidotus*.

Philothamnus hoplogaster (Günther, 1863)

Green Water Snake (Fig. 14, Map 12)

Material: PEM R23392, Malova Village next to Mipanha River, Huíla Province, -14.09140° 16.41476°, 1,569 m asl; PEM R23999, Lake Tchansengwe, Moxico, -12.41402° 18.64418°, 1,393 m asl; PEM R27375, Luvu River camp, Moxico Province, -13.71200° 21.83538°, 1,082 m asl. **Description:** Dorsal scales smooth and in 15 rows at midbody; 157–158 smooth ventrals; 79–88 paired subcaudals; 1 preocular; 2–3 postoculars; temporals 1+1; supralabials 8, with 4th and 5th entering the orbit; 9 infralabials, the first five in contact with the anterior



Map 12. Distribution of *Philothamnus hoplogaster* in Angola.



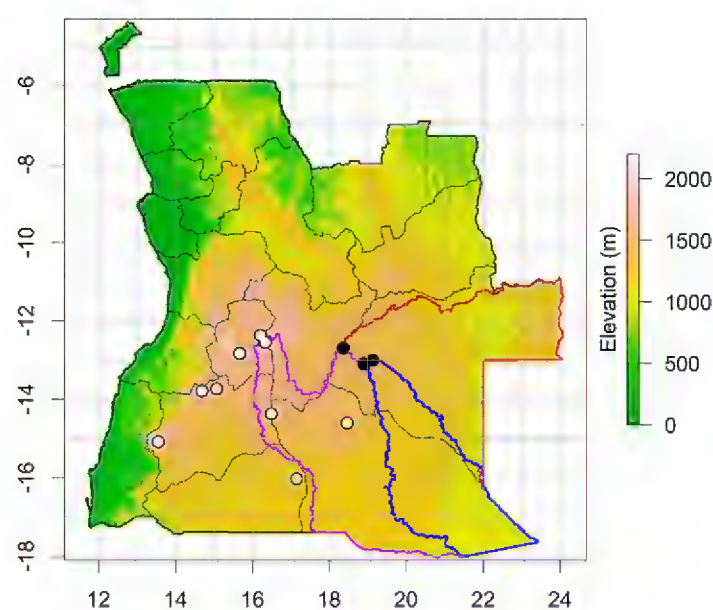
Fig. 15. *Philothamnus ornatus* from Cuito River source. Photo by Werner Conradie.

chin shield; cloacal scale divided. Largest female: 420 + 63 mm (PEM R27375); largest male: 290 + 130 mm (truncated; PEM R23992). **Habitat and natural history notes:** Found near waterbodies in Miombo woodland. One specimen had a *Kassina senegalensis* in its stomach. **Comment:** Among all the green snakes collected from the study area, only three specimens were assignable to typical *P. hoplogaster*. Often confused with *P. angolensis* and *P. heterolepidotus*, with which they share a similar temporal arrangement (1 + 1), but this species differs in the number of supralabials (2 vs. 3) entering the orbit and the absence of any ventral keeling (vs. weakly keeled in the other two). In a recent phylogenetic study of *Philothamnus*, a single Angolan sample was used from Lunda-Sul Province (Engelbrecht et al. 2019). These records represent the first for Moxico Province and south-eastern Angola, but records are known from adjacent western Zambia (Broadley 1971). This species was found sympatrically with *P. heterolepidotus* at Luvu River.

Philothamnus ornatus Bocage, 1872

Ornate Green Snake (Fig. 15, Map 13)

Material: PEM R23284–5, Cuanavale River source lake, Moxico Province, -13.09330° 18.89396°, 1,357 m asl; PEM R27376, Cuanavale River source lake, Moxico Province, -13.09052° 18.8939°, 1,357 m asl; PEM R23441–3, INBAC: WC-4806, Cuando River Source Trap 1, Moxico Province, -13.00393° 19.12808°, 1,351 m asl; PEM R23430–2, Cuando River Source Trap 2, Moxico Province, -13.00426° 19.12719°, 1,350 m asl; PEM R23330, Cuito River Source Lake, Moxico Province, -12.68935° 18.36012°, 1,435 m asl. **Description:** Dorsal scales smooth and in 15 rows at midbody; 146–159 smooth ventrals; 97–112 paired subcaudals; 1 preocular; 2 postoculars; temporals 1+1; supralabials 8, with 3rd–5th entering the orbit; 10 infralabials, the first five in contact with the anterior chin shield; cloacal scale divided. Largest female: 496 + 238 mm (PEM R23285); largest male: 412 + 126 mm (PEM R23431). **Habitat and natural history notes:** All specimens were found near waterbodies surrounded by grassland and mature



Map 13. Distribution of *Philothamnus ornatus* in Angola.

Miombo woodland. This species lacks ventral keeling and has never been observed climbing, unlike sympatric *P. heterolepidotus*. The stomachs of four snakes contained frogs of the genera *Ptychadena* and *Hyperolius*. **Comment:** *Philothamnus ornatus* was described by Bocage (1872) from two specimens collected at Huíla. Although subsequently recorded from Zambia and Zimbabwe (Broadley 1971; Broadley et al. 2003) and recently from Botswana (iNaturalist 35448603), it is known in Angola from only 10 localities (Marques et al. 2018). The species was recently documented for the first time from the Cuito River basin (Conradie et al. 2016), and here we document it from three more localities: Cuito River source, Cuanavale River source, and Cuando River source. These collections fill the gap between the records from western Angola and the Zambian populations.

Philothamnus semivariatus (Smith, 1840)

Spotted Bush Snake (Fig. 16, Map 14)

Material: PEM R23549, Quembo River source camp, Moxico Province, -13.14104° 19.05426°, 1,369 m asl; PEM R23563, west of Cuemba town, Moxico Province, -11.97027° 17.84878°, 1,319 m asl; PEM R24278, Cuando River, Camp 20, Moxico Province, -14.88452° 20.29548°, 1,116 m asl; PEM R27377, en route from Cangamba to Luio River, Moxico Province, -13.24037° 20.16443°, 1,312 m asl; PEM R27378, PEM R27379, INBAC: WC-7055, PEM R27380, Lake Hundo, Moxico Province, -14.97431° 21.62966°, 1,100 m asl. **Description:** Dorsal scales smooth and in 15 rows at midbody; 181–193 strongly keeled ventrals; 121–131 paired, keeled subcaudals; 1 preoculars; 2 postoculars; temporal formula variable, but mostly 2+2+2; supralabials 8–10, with mostly 4th–6th entering the orbit; 10 infralabials, the first five in contact with the anterior chin shield; cloacal scale divided. Largest female: 866 + 384 mm (PEM R27377); largest male: 847 + 367 (truncated) mm (PEM R23563). **Habitat and natural history notes:** All specimens exhibit distinct ventral keeling and were often encountered in elevated positions (arboreal) near waterbodies. Three individuals had *Hyperolius angolensis* in their stomachs. **Comment:**



Fig. 16. *Philothamnus semivariiegatus* from Quembo River source. Photo by Werner Conradie.

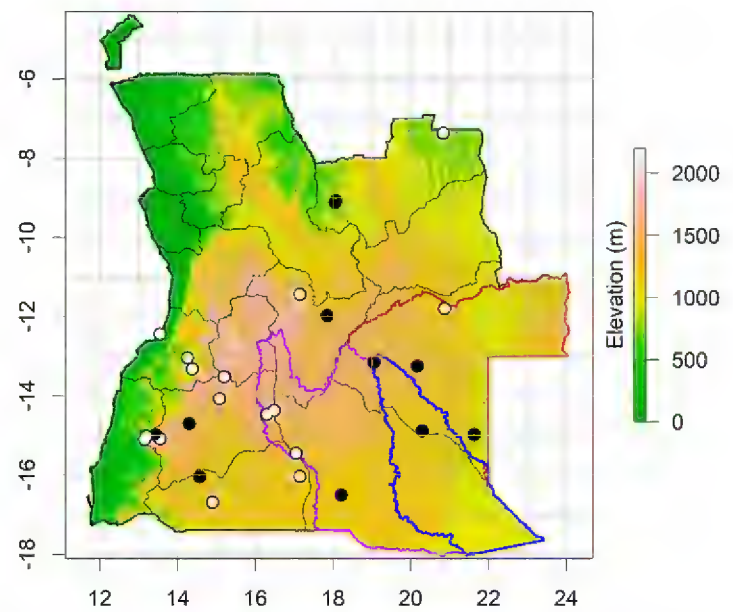
Material collected from the study area are uniform lime green without any black spots or bars, and have a yellow ventrum and ventral keeling. Recently, Engelbrecht et al. (2019) showed deep divergence within *P. semivariiegatus* and identified four distinct lineages. The material from Angola was grouped with the Central African clade, comprising mostly material from the DRC, Zambia, Zimbabwe, Mozambique, Namibia, and Tanzania. Further taxonomic work is needed to resolve the status of these four groups.

Thelotornis capensis oatesi (Günther, 1881)
Oates' Vine Snake (Fig. 17, Map 15)

Material: (photographic record only) Munhango region, Moxico Province, -12.17042° 18.55931°, ~1,443 m asl. **Comment:** Although Broadley (2001) distinguished *T. c. oatesi* based on head coloration and the high number of ventral scales, the status of this taxon was not fully resolved with phylogenetic analysis (Eimermacher 2012) and thus remains problematic. Our record represents the first record for Moxico Province, although this species is widespread within the country (Marques et al. 2018) and in adjacent western Zambia (Broadley 1971; Pietersen et al. 2017).



Fig. 17. *Thelotornis capensis oatesi* en route to Cuito River source, east of Muhango. Photo by Götz Neef.



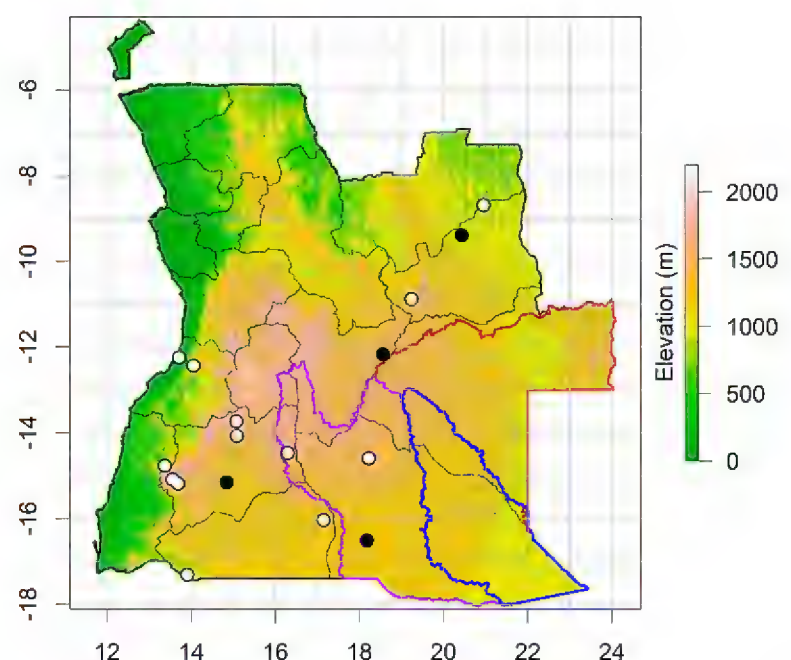
Map 14. Distribution of *Philothamnus semivariiegatus* in Angola.

Family: Natricidae

Limnophis bicolor (Günther, 1865)

Bicoloured Swamp Snake (Fig. 18, Map 16)

Specimens: PEM R23297, Delala River, near Samunanga village, Moxico Province, -12.93169° 18.81458°, 1,363 m asl; PEM R23454, Quembo River source trap 4, Moxico Province, -13.13586° 19.04709°, 1,368 m asl; PEM R23992, Rio Cuquema, upstream, Bié Province, -12.46902° 16.82415°, 1,640 m asl; PEM R24000, Upstream of Lungwebungu River bridge, Moxico Province, -12.56330° 18.64470°, ~1,307 m asl. **Description:** Dorsal scales smooth and in 19 rows at midbody; 127–136 smooth ventrals; 37–55 paired subcaudals; 1 preocular; 2 postoculars; temporals 1+2; parietal not touching the 6th supralabial, nasal sutures touching 1st supralabial; supralabials 8, with mostly 3rd and 4th entering the orbit; infralabials 9, with first five in contact with the anterior chin shield; cloacal scale divided. Largest female: 471 + 108 mm (PEM R23992); largest male: 333 + 93 mm (PEM R24000). **Habitat and natural history notes:** One specimen (PEM R23297) was observed swallowing a fish (*Tilapia sparrmanii* [Cichlidae]), which was regurgitated upon capture. Another specimen (PEM



Map 15. Distribution of *Thelotornis capensis oatesi* in Angola.



Fig. 18. *Limmophis bicolor* from Delala River, near Samunanga village. Photo by Werner Conradie.

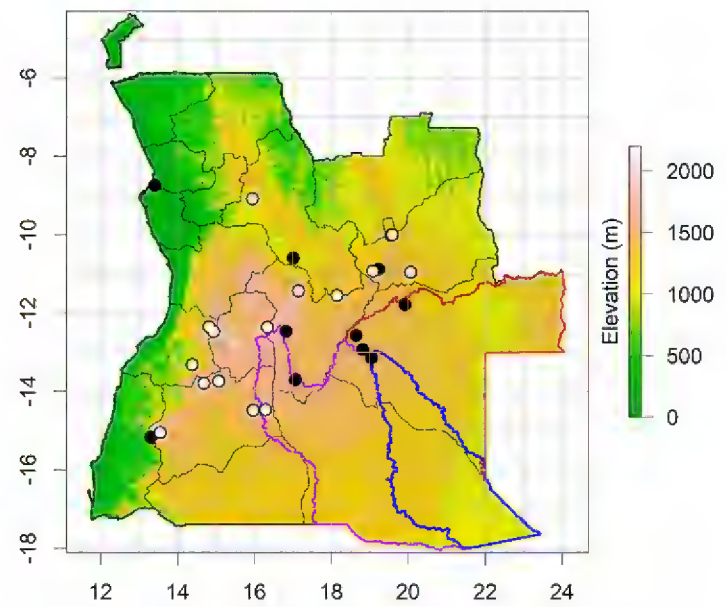
R2400) contained a suckermouth catlet (*Chiloglanis* sp.) in its stomach. All material are females, except PEM R2400. All females collected showed early egg development (March and April), except a female (PEM R23454) collected in November which contained eight well-developed eggs. **Comment:** The new material represents only the second set of published records for Moxico Province and the first for the Cuando River system (Laurent 1964; Conradie et al. 2020). *Limmophis bangweolicus* is also known to occur in eastern Moxico Province (Laurent 1964), and can easily be distinguished by different gular and subcaudal coloration patterns, head shape, and scalation (Conradie et al. 2020).

Natriciteres olivacea (Peters, 1854)
Olive Marsh Snake (Fig. 19, Map 17)

Material: PEM R27373, Lake Hundo, Moxico Province, -14.97431° 21.62966°, 1,100 m asl. **Description:** Dorsal scales smooth and in 19 rows at midbody; 140 smooth ventrals; 55 paired subcaudals; 2 preoculars; 3 postoculars; temporals 1+2; supralabials 8, with 4th and 5th entering the orbit; infralabials 9, with first five in contact with the anterior chin shield; cloacal scale divided. Female: 431 + 114 mm (PEM R27373). **Habitat and natural history notes:** A single gravid female was encountered being active at night at the edge of the lake



Fig. 19. *Natriciteres olivacea* from Lake Hundo. Photo by Werner Conradie.



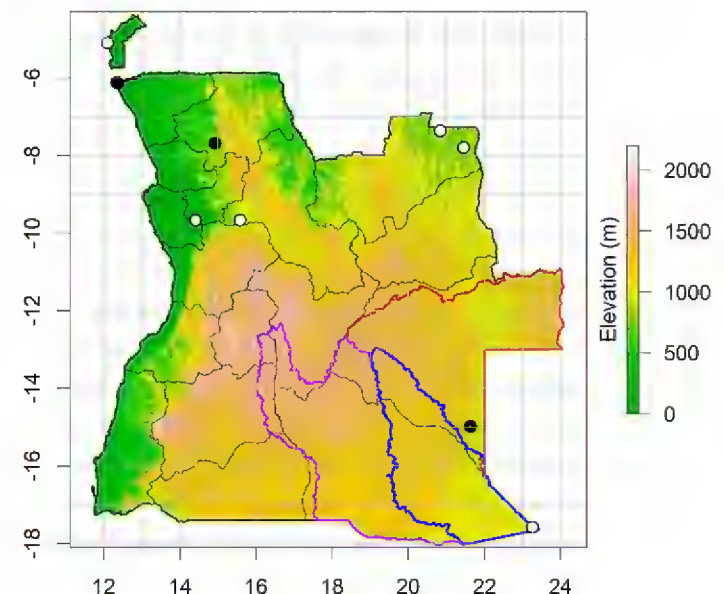
Map 16. Distribution of *Limmophis bicolor* in Angola.

surrounded by Miombo woodland. **Comment:** This new record represents the first record for Moxico Province and, overall, only the ninth record for Angola (Marques et al. 2018; Ernst et al. 2020). It is expected to be much more widely distributed, as it occupies habitat similar to that favored by *Limmophis bicolor*.

Superfamily: Elapoidea
Family: Atractaspididae
Subfamily: Aparallactinae

Amblyodipsas polylepis polylepis (Bocage, 1873)
Common Purple-glossed Snake (Fig. 20, Map 18)

Material: PEM R23535, EN280 West of Menongue, Cuando Cubango Province, -14.68858° 17.22208°, ~1,453 m asl. **Description:** Dorsal scales smooth and in 19 rows at midbody; 173 smooth ventrals; 26 paired subcaudals; 1 postocular; 2 temporals; 6 supralabials, the 3rd and 4th entering the orbit; 7 infralabials, the first five in contact with the anterior chin shield; cloacal scale divided. Male: 448 + 51 mm (PEM R23535). **Habitat and natural history notes:** An adult male was collected live on the road west of Menongue. **Comment:** This species is known from a handful of Angolan records (Marques et al. 2018). Recently, Portillo et al. (2018) used the above specimen in a phylogenetic study on the



Map 17. Distribution of *Natriciteres olivacea* in Angola.



Fig. 20. *Amblyodipsas polylepis polylepis* from west of Menongue. Photo by Luke Verburgt.

Aparallactinae and documented some genetic structure among the limited samples available to them. Loveridge (1944) divided *A. polylepis* into four distinct groups and documented the Angolan population to have a higher midbody scale row count. Our specimen had 17-19-19 scale rows, which conforms to the paratypes from Cazengo and Quissange (*vide* Broadley 1971). This represents the first record from south-eastern Angola, although it is known from adjacent Zambia, Namibia, and Botswana (Broadley 1971; Auerbach 1987; Broadley and Blaylock 2013).

Amblyodipsas ventrimaculata (Roux, 1907)

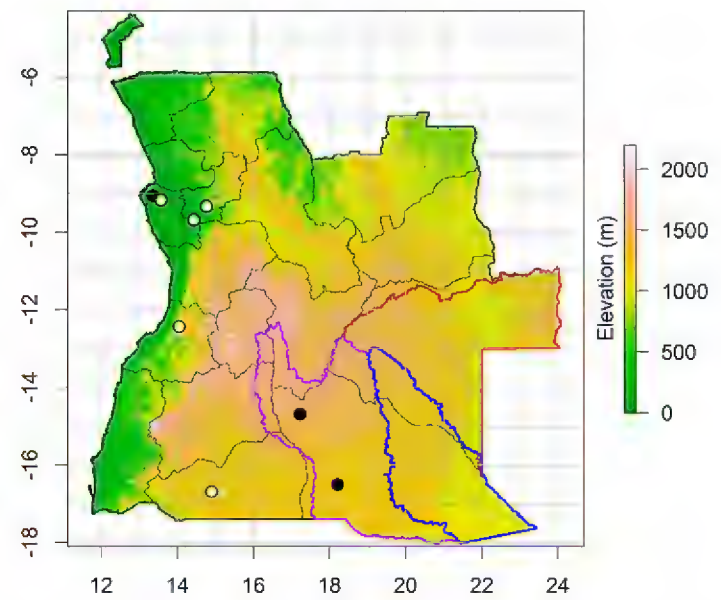
Kalahari Purple-glossed Snake (Fig. 21, Map 19)

Material: PEM R23320, Cuito River Source Lake, Moxico Province, -12.68935° 18.36012°, 1,435 m asl.

Description: Dorsal scales smooth and in 15 rows at midbody; 174 smooth ventrals; 19 paired subcaudals; 1 postocular; 1 temporal; 5 supralabials, with 2nd and 3rd entering the orbit; 5 infralabials, the first three in contact with the anterior chin shield; cloacal scale divided. Female: 266 + 20 mm (PEM R23320). **Habitat and natural history notes:** An adult female was collected in the grasslands above the Cuito River source. The snake contained three embryos. **Comment:** This specimen represents the first record of this species for



Fig. 21. *Amblyodipsas ventrimaculata* from Cuito River source. Photo by Werner Conradie.



Map 18. Distribution of *Amblyodipsas polylepis polylepis* in Angola.

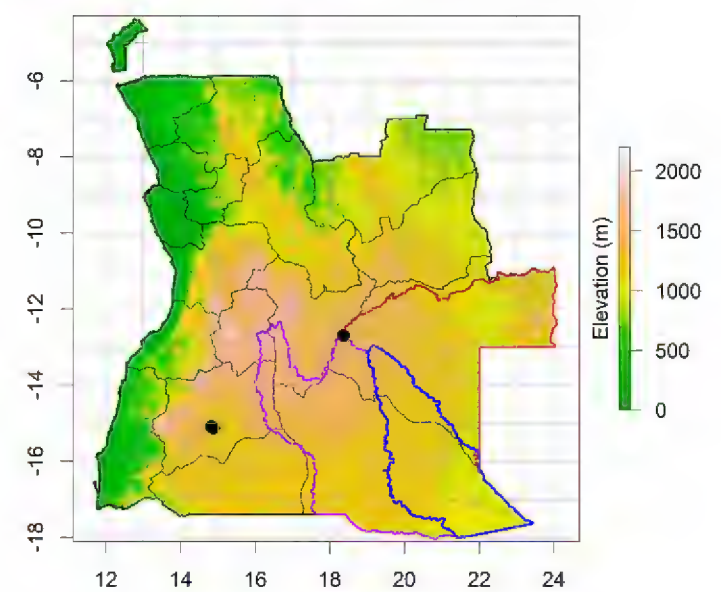
Angola (Branch 2018) and confirms the prediction of its occurrence in south-eastern Angola made by Conradie et al. (2016), which was based on the occurrence of suitable habitat and an abundance of food resources for the species. Recently, Portillo et al. (2018) used the specimen mentioned above and found no genetic differences between the Angolan population and the distant South African population. Butler et al. (2019) and Baptista et al. (2019a) documented the presence of this species from Bicular National Park in Huíla Province.

Xenocalamus mechowii Peters, 1881

Elongate Quill-snouted Snake (Fig. 22, Map 20)

Material: PEM R23463, Quembo River source, Moxico Province, -13.13586° 19.04709°, ~1,440 m asl; PEM R23533, alive on road, West of Menongue, Cuando Cubango Province, -14.67794° 17.23322°, 1,368 m asl; PEM R27385, grasslands west of Luo River, Moxico Province, -13.72468° 21.69403°, 1,009 m asl.

Description: Dorsal scales smooth and in 17 rows at midbody; 228–254 smooth ventrals; 27–28 paired subcaudals; 2 postoculars; 1 temporal; 6 supralabials, the 3rd and 4th entering the orbit; 5 infralabials, the first two in contact with the anterior chin shield; cloacal scale divided. Largest male: 438 + 40 mm (PEM R23533). **Habitat and natural history notes:** PEM R23463 had the remains of



Map 19. Distribution of *Amblyodipsas ventrimaculata* in Angola.



Fig. 22. *Xenocalamus mechowii* from west of Menongue. Photo by Luke Verburgt.

a *Zygaspis nigra* in its stomach. **Comment:** Broadley (1971) assigned material from western Zambia to a hybrid form between the two subspecies, *X. m. mechowii* and *X. m. inornatus*, due to scale counts overlapping with the two recognized subspecies. Our northernmost specimen has scalation within the range of *X. m. inornatus* (PEM R23463 and PEM R27385: 247 and 254 ventrals and 27 and 28 subcaudals), while our southern sample is in range of *X. m. mechowii* (PEM R23533: 228 ventrals and 28 subcaudals) and thus could also be allocated to these transitional populations. Recently, Portillo et al. (2018) used the material mentioned above and found no genetic differences between the two samples, but that study did not include material from the northern populations of the nominal form (i.e., outside of the purported hybrid zone). These inconsistencies in morphology coupled with low genetic divergence cast doubt on the validity of these two subspecies. Further investigation is needed to assess the validity of the taxa in question, but here we treat them by their binomial name.

Family: Lamprophiidae

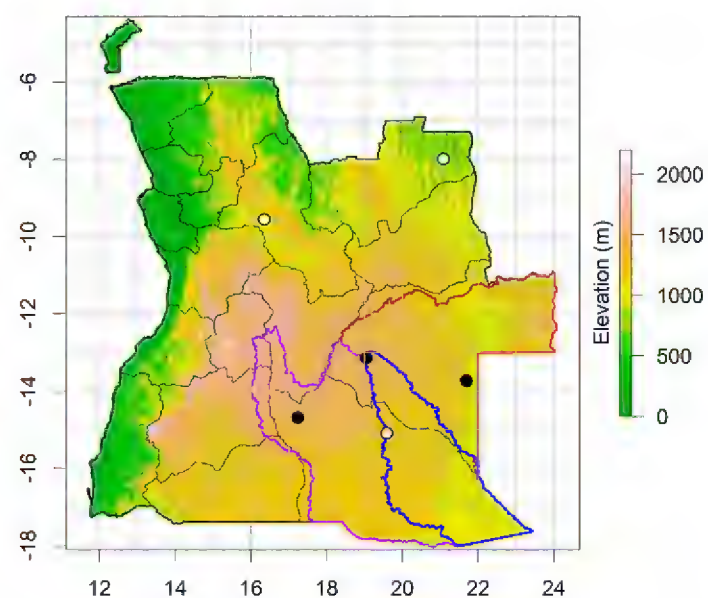
Boaedon angolensis Bocage, 1895

Angolan House Snake (Fig. 23, Map 21)

Material: PEM R23251, 65 km south of Menongue (DOR), Cuando Cubango Province, -15.26050°



Fig. 23. *Boaedon angolensis* from west of Menongue. Photo by Luke Verburgt.



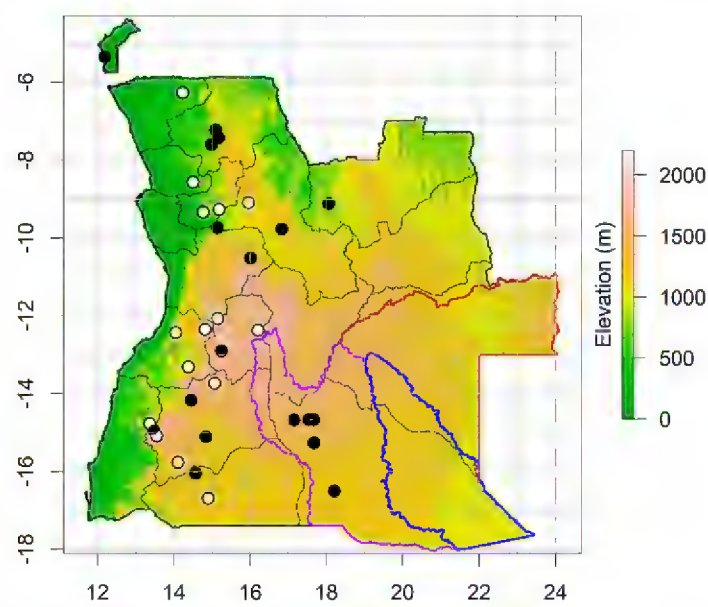
Map 20. Distribution of *Xenocalamus mechowii* in Angola.

17.677614°, 1,246 m asl; PEMR23403, Menongue HALO compound, Cuando Cubango Province, -14.66313° 17.66522°, 1,385 m asl; PEM R23536, 60 km West of Menongue on EN280, Cuando Cubango Province, -14.67253°, 17.14700°, 1,378 m asl. **Description:** Dorsal scales smooth and in 28 rows at midbody; 203–224 smooth ventrals; 51–67 paired subcaudals; 1 preocular; 2 postoculars; temporals 1+2; 8 supralabials, the 4th and 5th entering the orbit; 9 infralabials, the first four in contact with the anterior chin shield; cloacal scale divided. Largest female: 882 + 134 mm (PEM R23403); largest male: 460 + 140 mm (PEM R23251). **Habitat and natural history notes:** Specimens were only found in the Cubango River drainage. **Comment:** The name *Boodon lineatus* var. *angolensis* Bocage, 1895 was reinstated for most of the material from central and western Angola (Hallermann et al. 2020). This species is widespread in Angola and endemic to the country.

Boaedon branchi Hallermann, Ceriaco, Schmitz, Ernst, Conradie, Verburgt, Marques, and Bauer, 2020

Branch's House Snake (Fig. 24, Map 22)

Material: PEM R21846, 47.5 km E of Menongue on road to Cuito Cuanavale, Cuando Cubango Province, -14.59517° 18.07111°, 1,497 m asl; PEM R23538, Longa River, Cuando Cubango Province, -14.55956° 18.41406°, 1,319 m asl. **Description:** Dorsal scales smooth and in



Map 21. Distribution of *Boaedon angolensis* in Angola.

Snakes of the Okavango Delta headwater area in Angola



Fig. 24. *Boaedon branchi* from Longo River east of Menongue. Photo by Bill Branch.

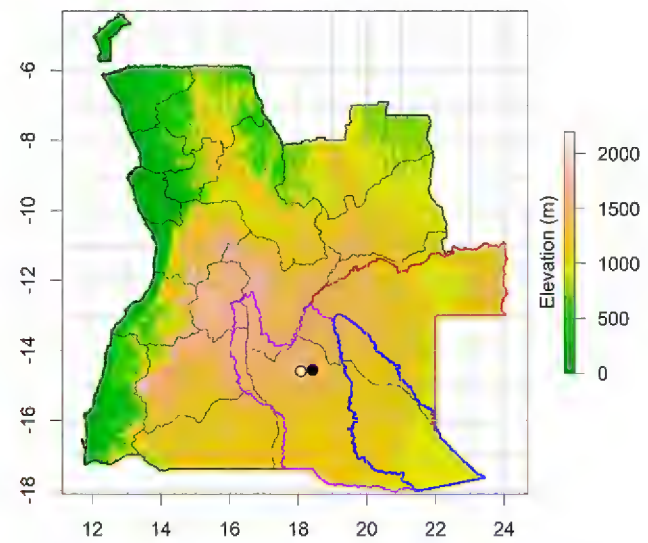
29 rows at midbody; 197 and 210 smooth ventrals; 64 and 67 paired subcaudals; 1–2 preoculars; 2 postoculars; temporals 1+2; 8 supralabials, the 4th and 5th entering the orbit; 9 infralabials, the first four in contact with the anterior chin shield; cloacal scale divided. Largest male: 508 + 123 mm (PEM R21846). **Habitat and natural history notes:** The stomach of the subadult male contained an unidentified rodent. **Comment:** The unusual pale-yellow specimen previously identified as *Boaedon* cf. *angolensis* in Conradie et al. (2016, Fig. 9G) is here referred to as the recently described *Boaedon branchi*, which is only known from two specimens from east of Menongue, Cuando Cubango Province (Hallermann et al. 2020).

Boaedon fradei Hallermann, Ceriaco, Schmitz, Ernst, Conradie, Verbugt, Marques, and Bauer, 2020
Zambezi/Frade's House Snake (Fig. 25, Map 23)

Material: PEM R23486–7, Quembo River source lake, Moxico Province, -13.13544° 19.04397°, 1,375 m asl; PEM R23985, bridge over Lungwebungu River, Moxico Province, -12.58013° 18.66740°, 1,304 m asl; PEM R25338, Lake Hundo, Moxico Province, -14.97431° 21.62966°, 1,100 m asl; PEM R27746, lower Cuando River, -16.50574° 22.10673°, 1,023 m asl. **Description:** Dorsal scales smooth and in 28–29 rows at midbody; 201–214 smooth ventrals; 50–74 paired subcaudals; 1 preocular; 2 postoculars; temporals mostly 1+2+3; 8



Fig. 25. *Boaedon fradei* from Quembo River source. Photo by Werner Conradie.

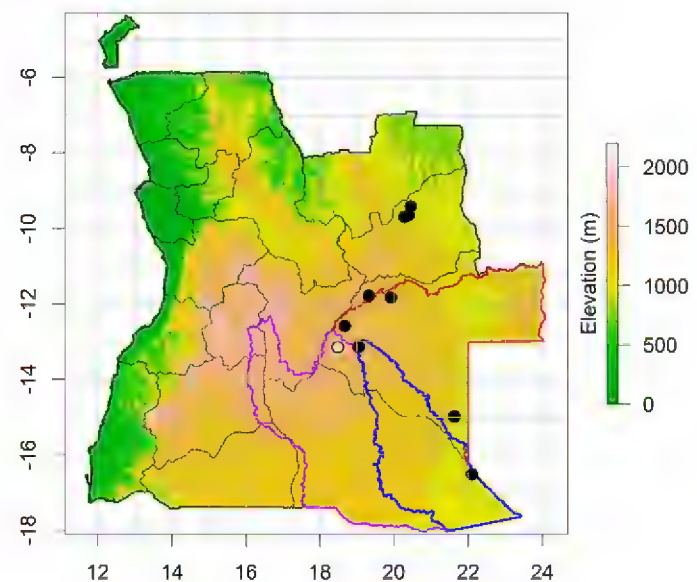


Map 22. Distribution of *Boaedon branchi* in Angola.

supralabials, 3rd–5th entering the orbit; 9 infralabials, the first four in contact with the anterior chin shield; cloacal scale entire. Largest female: 738 + 122 mm (PEM R23486); largest male: 608 + 143 mm (PEM R23985). **Habitat and natural history notes:** All specimens were associated with Angolan Miombo Woodland and Zambezian *Baikiaea* woodlands. **Comment:** Material collected from this study comprised the type series of the newly described *B. fradei* from eastern Angola (Hallermann et al. 2020). A photographic record mentioned in the text of Conradie et al. (2016) under the heading *Boaedon* cf. *angolensis* can be assigned to this new species based on overall coloration and distribution (see iNaturalist 1727921). *Boaedon fradei* is widespread in the southern DRC, and is found throughout western and northern Zambia to the Zambezi Region (= Caprivi Strip) in Namibia and adjacent Botswana (Conradie et al., In Prep.)

Lycophidion multimaculatum Boettger, 1888
Spotted Wolf Snake (Fig. 26, Map 24)

Material: PEM R23399, Cubango River Source Site, Huambo Province, -12.66388° 16.09385°, 1,771 m asl; PEM R23455, Quembo trap 4, Moxico Province, -13.13586° 19.04709°, 1,368 m asl; PEM R23467–8, Quembo trap 1, Moxico Province, -13.13592° 19.04417°, 1,369 m asl. **Description:** Dorsal scales smooth and in 17 rows at midbody; 160–176 smooth ventrals; 22–27 paired



Map 23. Distribution of *Boaedon fradei* in Angola.



Fig. 26. *Lycophidion multimaculatum* from Quembo River source. Photo by Werner Conradie.

subcaudals; 2 postoculars; temporals mostly 1+2+3; 8 supralabials, the 3rd–5th entering the orbit; 8 infralabials, the first four in contact with the anterior chin shield; cloacal scale entire. Largest female: 446 + 37 mm (PEM R23399); largest male: 236 + 38 mm (PEM R23468). **Habitat and natural history notes:** Stomach contents of two snakes contained *Trachylepis* and *Ichnotropis* remains. One female (PEM R23467; collected 3 Nov 2016) contained five fully developed eggs. **Comment:** Broadley (1996) reassigned all historical *L. capense* material from Angola to *L. multimaculatum*. Elsewhere, this species is widely distributed in western and northern Zambia (Broadley 1971; Broadley et al. 2003) and the Zambezi Region (= Caprivi Strip) of Namibia (Branch 1998).

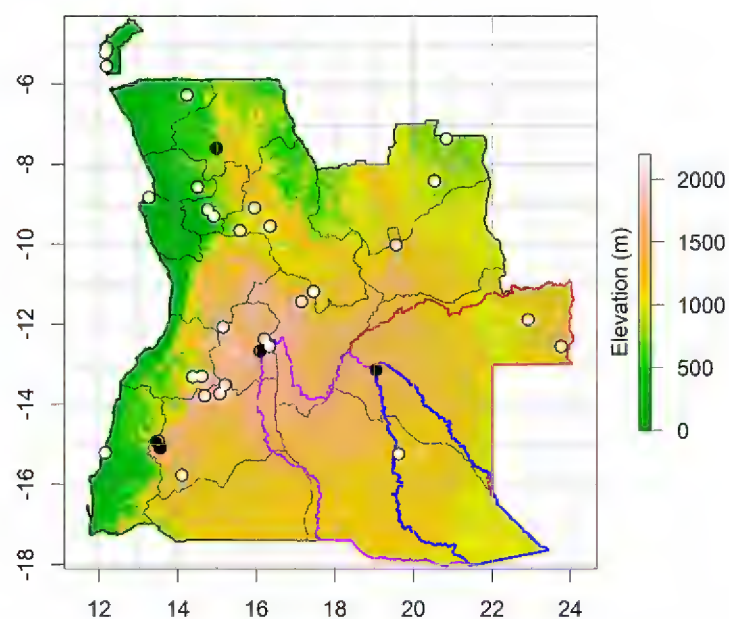
Family: Prosymnidae

Prosymna angolensis Boulenger, 1915
Angola Shovel-snout Snake (Fig. 27, Map 25)

Material: PEM R27381, Quembo River bridge camp, Trap 4, Moxico Province, -13.52658° 19.27810°, 1,248 m asl; PEM R23456–8, Quembo trap 4, Moxico Province, -13.13586° 19.04709°, 1,368 m asl; PEM R23483, Cuando River Source Trap 4, Moxico Province, -13.00164° 19.1296°, 1,372 m asl; PEM R23510–2, Cuito

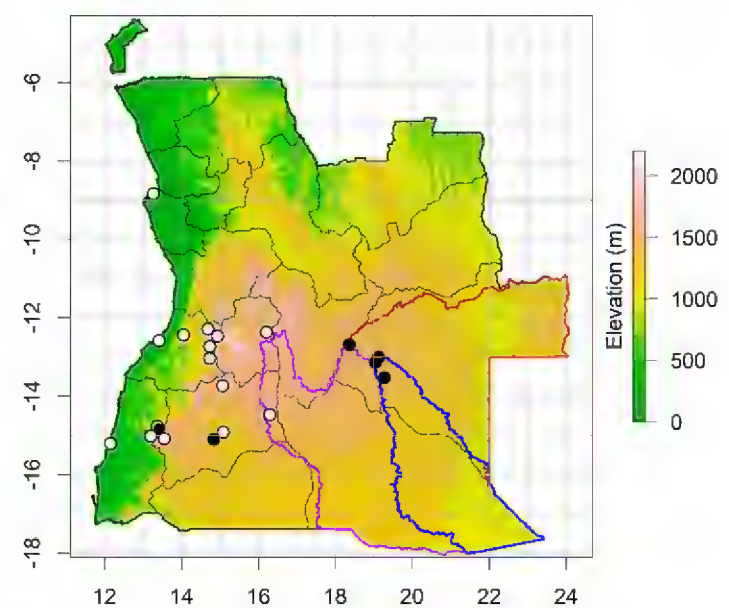


Fig. 27. *Prosymna angolensis* from Cuando River source. Photo by Werner Conradie.



Map 24. Distribution of *Lycophidion multimaculatum* in Angola.

Source Lake, Moxico Province, -12.68866° 18.36025°, 1,426 m asl. **Description:** Dorsal scales smooth and in 15 rows at midbody; 116–124 smooth ventrals; 18–26 paired subcaudals; 1 (rarely 2) preoculars; 2 postoculars; temporals mostly 1+2; 6 supralabials, with 2nd–4th entering the orbit; 7 infralabials, the first three in contact with the anterior chin shield; cloacal scale entire; 21–36 fused dark dorsal spots. Largest female: 200 + 21 mm (PEM R23456); largest male: 198 + 25 mm (PEM R23458). **Habitat and natural history notes:** All specimens were captured in traps in sandy areas next to source lakes. **Comment:** Boulenger (1915) described this species from Angola, but did not designate a precise type locality. Loveridge (1958) was the first to propose designating Huíla as the type locality, but it was Broadley (1980) that finally restricted it to Caconda, since the Huíla material could not be found. This species is mostly distributed in central and western Angola, with isolated records from western Zambia, the Zambezi Region (=Caprivi Strip) in north-eastern Namibia, and northern Botswana (Broadley 1980). Material from south-eastern Angola exhibits the same dorsal coloration (large black fused blotches, similar to *P. janii*, which is restricted to Mozambique and north-eastern South Africa), lower ventral and subcaudal scale counts, and two postoculars as described for specimens from western Zambia, which



Map 25. Distribution of *Prosymna angolensis* in Angola.



Fig. 28. *Kladiostratus acutus* from Cuando River source. Photo by Werner Conradie.

differ from the type material from Caconda (Broadley 1980). Despite these differences, Broadley (1980) did not make any taxonomic changes but stated that a larger series was needed to resolve this issue. The taxonomic status of this material is under investigation, and it may prove to be a separate species from the western and southern populations.

Family: Psammophiidae

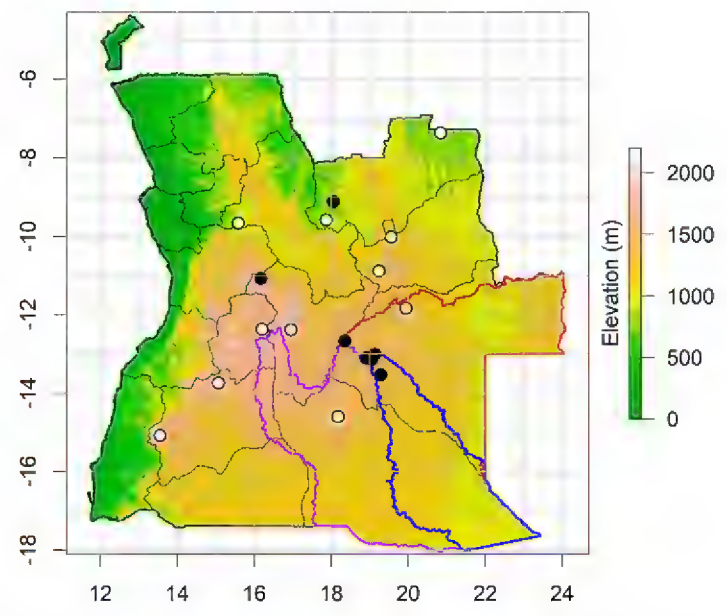
Kladiostratus acutus (Günther, 1888)

Branch's Beaked Snake (Fig. 28, Map 26)

Material: PEM R23496, Cuanavale River source lake, Moxico Province, -13.09442° 18.89372°, 1,396 m asl; PEM R23288, Cuanavale River source lake, Moxico Province, -13.09330° 18.89396°, 1,367 m asl; PEM R23445–6, Cuando River Source Trap 1, Moxico Province, -13.00393° 19.12808°, 1,351 m asl; PEM R23434–6, Cuando River Source Trap 2, Moxico Province, -13.00426° 19.12719°, 1,350 m asl; PEM R23449–50, Cuando River Source Trap 3, Moxico Province, -13.00334° 19.13564°, 1,364 m asl; PEM R23315, Cuito River Source Lake, Moxico Province, -12.66825° 18.35282°, 1,407 m asl; PEM R27371, Quembo River bridge camp, Trap 1, Moxico Province, -13.528005° 19.281466°, 1,236 m asl; PEM R23476, Quembo trap 1, Moxico Province, -13.13592° 19.04417°,



Fig. 29. *Psammophis jallae* from west of Cuanavale River source. Photo by Werner Conradie.



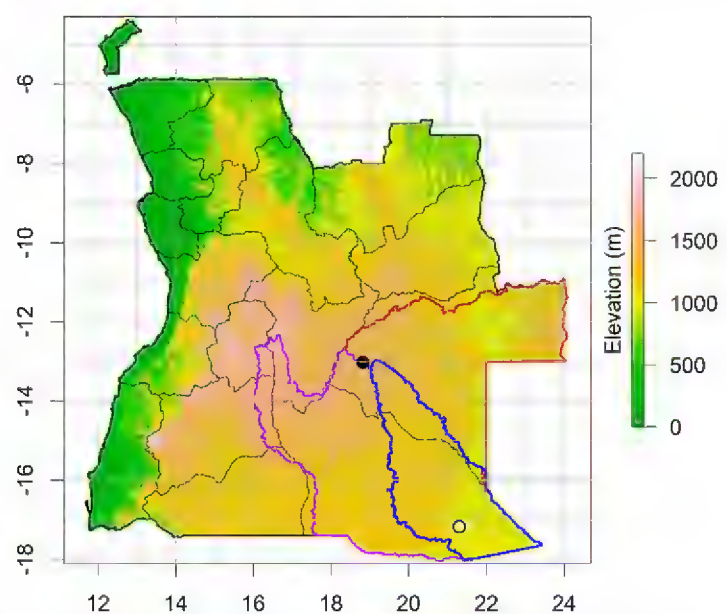
Map 26. Distribution of *Kladiostratus acutus* in Angola.

1,369 m asl; PEM R23459, INBAC: WC-4726, Quembo trap 4, Moxico Province, -13.13586° 19.04709°, 1,368 m asl. **Description:** Dorsal scales smooth and in 17 rows at midbody; 170–189 smooth ventrals; 57–72 paired subcaudals; 1 preocular; 2 postoculars; temporals mostly 2+3; 8 supralabials, the 4th and 5th entering the orbit; 9 infralabials, the first five in contact with the anterior chin shield; cloacal scale divided. Largest specimen: 677 + 170 mm (male, PEM R23315). **Habitat and natural history notes:** One specimen had some mammal hair in the stomach, while others contained frogs (*Hyperolius* sp., *Breviceps ombelanonga*, and *Kassina senegalensis*). **Comment:** A widespread species recorded mostly from the Angolan plateau (Marques et al. 2018). Manaças (1973) was the first to record this species from Moxico Province under the name *Psammophis acutus*. We recorded numerous new records for Moxico Province, and the new material formed the basis of the description of the new genus *Kladiostratus* (Keates et al. 2019). The status of *K. a. jappi* from adjacent Zambia, and whether its distribution extends into eastern Angola, still need to be clarified (Broadley 1971).

Psammophis jallae Peracca, 1896

Jalla's Sand Snake (Fig. 29, Map 27)

Material: PEM R23523, just west of Cuanavale River source (DOR), Moxico Province, -13.01347° 18.81669°,



Map 27. Distribution of *Psammophis jallae* in Angola.



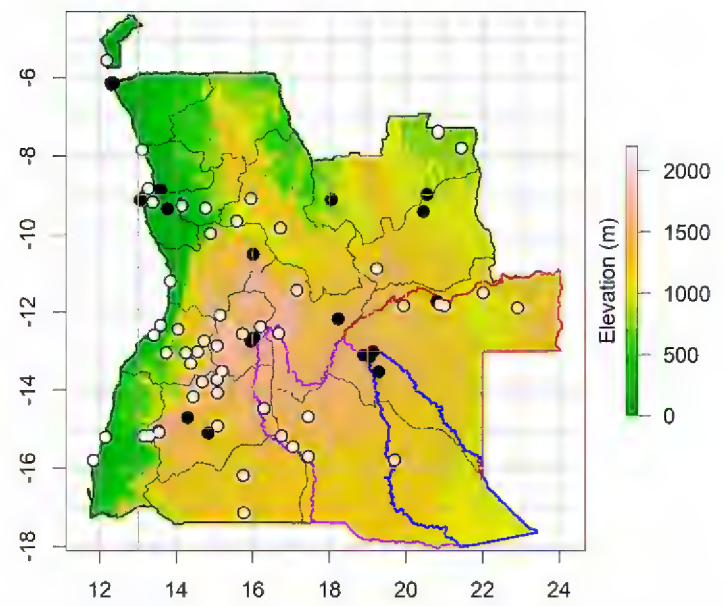
Fig. 30. *Psammophis mossambicus* from Quembo River source. Photo by Werner Conradie.

153 m asl. **Description:** Dorsal scales smooth and in 15 rows at midbody; 176 smooth ventrals; 97 paired subcaudals; 1 preocular; 2 postoculars; temporals 2+3+3; 7 supralabials, the 3rd and 4th entering the orbit; 9 infralabials, the first four in contact with the anterior chin shield; cloacal scale divided. Female: 460 + 191 mm (PEM R23523). **Habitat and natural history notes:** Single specimen collected DOR with adjacent open grassland. The specimen had an *Ichnotropis* sp. in its stomach. **Comment:** This is only the second record of the species for Angola. The only other record from Angola is from Lumuna River (Angel 1921). Marques et al. (2018) incorrectly assigned the material from Bigondo and ‘Benguella to Bihe,’ recorded by Loveridge (1940), to *P. jallae*, when in fact it actually refers to the *P. ansorgii* material reported by Boulenger (1905; see Branch et al. 2019). The former locality is not mentioned in Boulenger (1905), but Monard (1937b) implied that it originated from Boulenger (1905). At that stage, Loveridge (1940) regarded *P. ansorgii* as a junior synonym of *P. jallae*. Later, Broadley (1977) reinstated both as valid species. Loveridge (1940) also synonymized Angel’s (1921) *P. rohani* with *P. jallae*, and this was followed by subsequent authors (Broadley 1977).

Psammophis mossambicus Peters, 1882

Olive Grass Snake (Fig. 30, Map 28)

Material: PEM R23402, DOR near Katchiungo, Huambo Province, -12.65341° 16.02845°, 1,828 m asl; PEM R23286, Cuanavale River source lake, Moxico Province, -13.09330° 18.89396°, ~1,367 m asl; PEM R23448, Cuando River Source Trap 3, Moxico Province, -13.00334° 19.13564°, 1,364 m asl; PEM R23491, Quembo trap 2, Moxico Province, -13.13544° 19.04397°, 1,375 m asl; PEM R27382, Quembo River bridge camp, Trap 2, Moxico Province, -13.52816° 19.28067°, 1,240 m asl; INBAC: WC-5186, DOR 1, near Cauanga, -12.73778° 15.94731°, 1,777 m asl. **Description:** Dorsal scales smooth and in 17 rows at midbody; 162–174 smooth ventrals; 81–98 paired subcaudals; 1 preocular; 2 postoculars; temporals mostly 2+3 or



Map 28. Distribution of *Psammophis mossambicus* in Angola.

2+3+3; 8 supralabials, the 4th and 5th entering the orbit; 10 infralabials, the first four in contact with the anterior chin shield; cloacal scale divided. Largest female: 867 + 350 mm (PEM R20024); largest male: 1,000 + 398 mm (PEM R23286). **Habitat and natural history notes:** The remains of *Trachylepis* sp. and *Panaspis* sp. were found in the stomachs of two of the specimens. **Comment:** Although Trape et al. (2019) recently made substantial progress in resolving most of the taxonomical issues surrounding the *P. sibilans* complex, historical Angolan material assigned to either *P. brevirostris*, *P. leopardinus*, *P. mossambicus*, *P. phillipsi*, or *P. sibilans* needs to be re-examined and genetically assessed (Conradie et al. 2016).

Psammophis zambiensis Hughes and Wade, 2002

Zambian Whip Snake (Fig. 31, Map 29)

Material: PEM R23287, Cuanavale River source lake, Moxico Province, -13.09330° 18.89396°, ~1,367 m asl; PEM R23444, INBAC: WC-4793, Cuando River Source Trap 1, Moxico Province, -13.00393° 19.12808°, 1,351 m asl; PEM R23433, Cuando River Source Trap 2, Moxico Province, -13.00426° 19.12719°, 1,350 m asl; PEM R23331, Cuito River Source Lake, Moxico Province, -12.68935° 18.36012°, 1,435 m asl; PEM R27384, Quembo River bridge camp, Trap 4, Moxico Province, -13.52658° 19.27810°, 1,248 m asl; PEM R23475, Quembo trap 1, Moxico Province, -13.13592° 19.04417°, 1,369 m asl. **Description:** Dorsal scales smooth and in 17 rows at midbody; 150–160 smooth ventrals; 75–86 paired subcaudals; 1 preocular; 2 postoculars; temporals 2+3; 8 supralabials, with 4th and 5th entering the orbit; 9 infralabials, the first four in contact with the anterior chin shield; cloacal scale divided. Largest female: 524 + 78 mm (PEM R23433); largest male: 656 + 237 mm (PEM R23444). **Habitat and natural history notes:** One specimen had a *Ptychadena uzungwensis* in its stomach, while another contained the remains of a *Trachylepis* sp. **Comment:** This species was only recently described from northern Zambia and adjacent DRC (Hughes and Wade 2002), and very little is



Fig. 31. *Psammophis zambiensis* from Cuando River source. Photo by Werner Conradie.

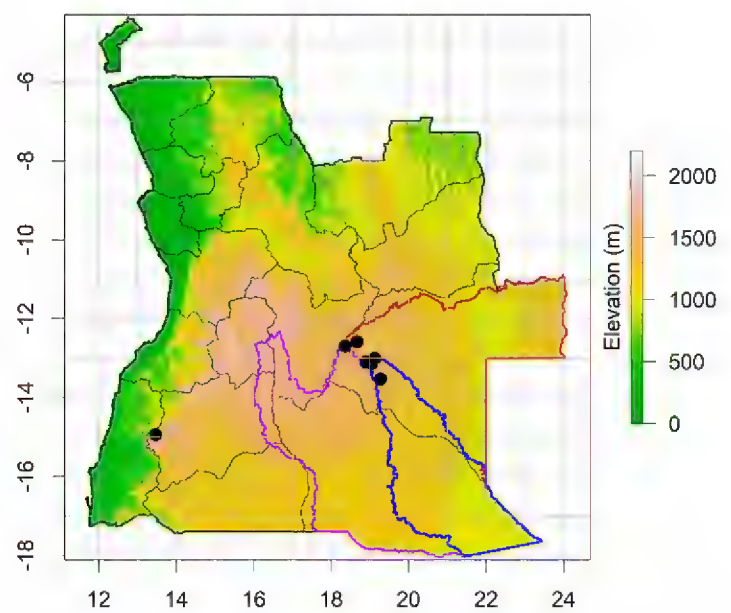
known about its full distribution. These new records are the first confirmed records of *P. zambiensis* for Angola and extend the species' distribution westward. Marques et al. (2018) assigned material from Calombe (Mananças 1973), Dundo (Laurent 1950, 1954, 1964; Thys van den Audenaerde 1966), 'Dundo, R. Mussungue, aff. Luachimo' (Thys van den Audenaerde 1966), 'Barrage de la Luachimo' (Thys van den Audenaerde 1966), and 'Muita (Lumebe)' (Laurent 1954) as potentially belonging to this species, but the ventral (168–177) and subcaudal (83–98) counts listed are much higher than those recorded by Hughes and Wade (2002; 148–165 ventrals and 75–90 subcaudals) for *P. zambiensis* and groups closer with the *P. 'sibilans'* group (e.g., 167–177 ventrals and 81–103 subcaudals). In addition to the lower scale counts, this species has diagnostic ventral black barring which distinguishes it from the sympatric *P. mossambicus* (Hughes and Wade 2002). A genetically confirmed record from Lubango, Huíla Province (PEM R22074) extends the known distribution of this species 600 km further west (Keates 2021). It has also recently been recorded as far east as Malawi (Brown 2019).

Family: Elapidae

Dendroaspis polylepis Günther, 1864
Black Mamba (Fig. 32, Map 30)

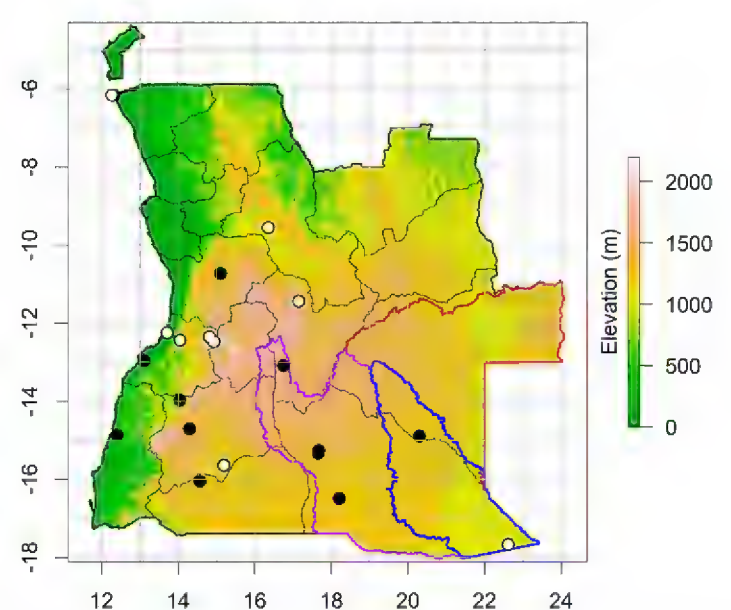


Fig. 32. *Dendroaspis polylepis* from Cuando River. Photo by Götz Neef.



Map 29. Distribution of *Psammophis zambiensis* in Angola.

Material: PEM R24277, Cuando River, Camp 20, Moxico Province, -14.88452° 20.29548° , ~1,116 m asl; DOR (photo and DNA), near Caiundo, Cuando Cubango Province, -15.32121° 17.651610° , ~1,306 m asl; LVA2 (DNA), EN140 north of Menongue, Cuando Cubango Province, -13.08367° 16.75083° , ~1,710 m asl. **Additional photographic records:** Cuatir, Cuando Cubango Province, -16.48523° 18.20304° , Stefan van Wyk; Menongue, Cuando Cubango Province, -14.63015° 17.63465° , Stefan van Wyk. **Description:** Dorsal scales smooth and in 21 rows at midbody; 273 smooth ventrals; 121 paired subcaudals; 3 preoculars; 4 postoculars; temporals mostly 1+2; 8 supralabials, the 4th entering the orbit; 12 infralabials, the first four in contact with the anterior chin shield; cloacal scale divided. Female: 1,570 + 460 mm (PEM R24277). **Habitat and natural history notes:** The specimen from Cuando River shared a hole with a *Philothamnus semivariiegatus* (PEM R24278). Two adult specimens were seen mating near the Khula River source in April 2017. **Comment:** Two species of Mamba are known to occur in Angola, *D. jamesoni* and *D. polylepis* (Branch 2018; Marques et al. 2018). Most historical material of *D. polylepis* from Angola was wrongly referred to as *D. angusticeps* (see citations within Marques et al. 2018), which was only rectified by Bayhman (2010). Fewer than 10 records of *D. polylepis* were mapped in Marques et al. (2018).



Map 30. Distribution of *Dendroaspis polylepis* in Angola.

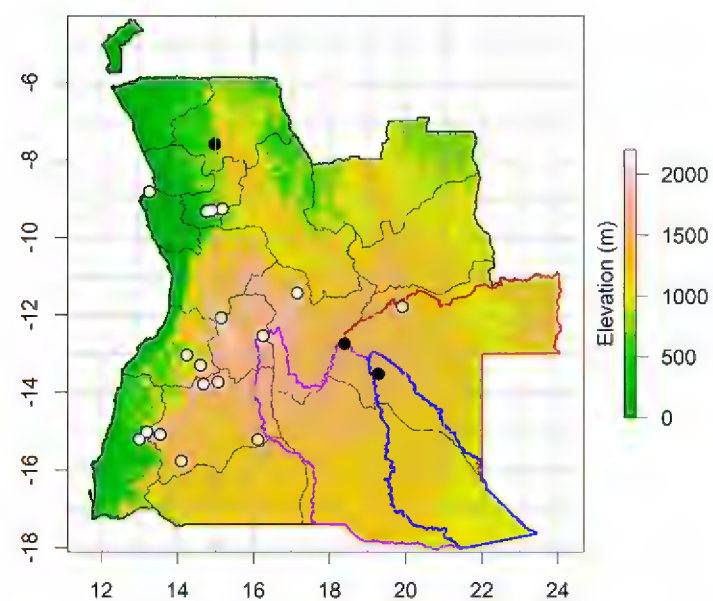


Fig. 33. *Elapsoidea semiannulata semiannulata* from Quembo River bridge site. Photo by Werner Conradie.

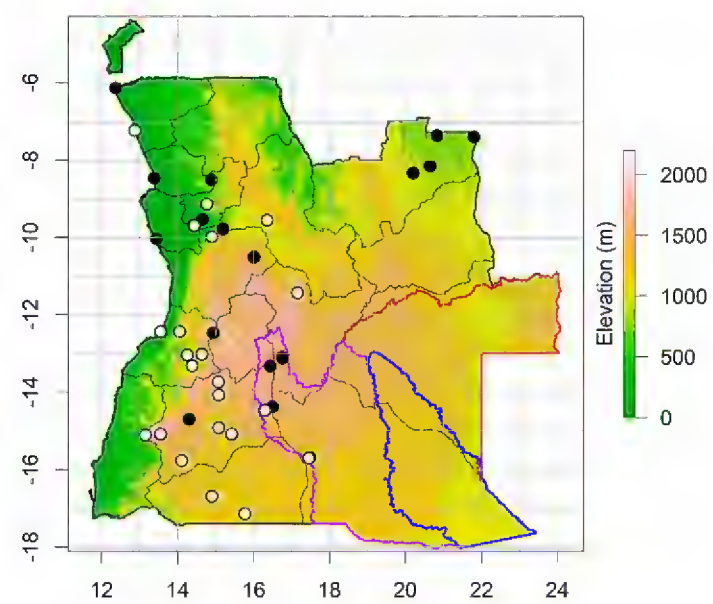
Since then, numerous new records have been documented from Angola (Baptista et al. 2019a; iNaturalist 32281228, 32523446; this study). As predicted by Conradie et al. (2016), this species appears to be widespread in central and southern Angola, with an isolated record from the extreme north-western section of Angola (Bayhman 2010). The record mapped in Marques et al. (2018) from Lake Carumbo, Lunda-Norte Province is based on a sight record that cannot be properly verified to the species level (Branch and Conradie 2015). It should thus be omitted until new material can be collected, and the validity of the record confirmed. The absence of this species from north-eastern Angola is further supported by Laurent (1950, 1954, 1964) and Thys van den Audenaerde (1966) who failed to document this species in their extended works.

Elapsoidea semiannulata semiannulata Bocage, 1882
Angolan Garter Snake (Fig. 33, Map 31)

Material: PEM R23561, en route to Kulu River source, approx. -12.73915° 18.39236° , 1,453 m asl; PEMR27370, lower Quembo River, -13.52988° 19.28340° , 1,242 m asl. **Description:** Dorsal scales smooth and in 13 rows at midbody; 146 and 148 smooth ventrals; 23 and 25 paired subcaudals; 1 preocular; 2 postoculars; temporals 1+2; 7 supralabials, 3rd and 4th entering the orbit; 7 infralabials, the first four in contact with the anterior chin shield (4th in narrow contact); cloacal scale divided. Thirty faint bands present on the dorsum, extending onto the flanks but absent from the venter. Largest male: 393 + 43 mm (PEM R27370). **Habitat and natural history notes:** Members of the logistic team stumbled upon a scene where a larger unidentified snake was busy consuming a smaller snake (*Elapsoidea s. semiannulata*). The larger snake then regurgitated its prey and disappeared into the bush. The second specimen was found active at night in grassland next to the Quembo River. **Comment:** This material represents only the second and third record for Moxico Province. The only other record for the country is from 200 km northeast of Lunea = Vila Luso (Manaças 1981). Outside of Angola, the species is known from Zambia west of the Zambezi River and northern Namibia (Broadley 1971).



Map 31. Distribution of *Elapsoidea semiannulata semiannulata* in Angola.



Map 32. Distribution of *Naja (Afronaja) nigricollis* in Angola.

Naja (Afronaja) nigricollis (Reinhardt, 1843)

Black-necked Spitting Cobra (Map 32)

Material: PEM R23250, near Caiundo, Cuando Cubango Province, -15.68460° 17.47872° , 1,190 m asl; PEM R23556, EN140 North of Menongue, Bié Province, -13.08633° 16.75083° , ~1,710 m asl. **Description:** Dorsal scales smooth and in 19 rows at midbody; 188 smooth ventrals; 62 paired subcaudals; 1 or 2 preoculars; 3 postoculars; temporals 2+4 and 2+5; supralabials 6, the 3rd entering the orbit; 8 infralabials, the first four in contact with the anterior chin shield; cloacal scale entire. Male: 311 + 24 mm (PEM R23561). For PEM R23250 we only have the head. **Habitat and natural history notes:** Both specimens had mammal hair in the gut or in their mouths. **Comment:** It is a widespread species in central and western Angola (Marques et al. 2018). The only specimens we encountered were in the western part of the study area, associated with drier Miombo woodlands. They seem to be absent from the wetter Miombo woodlands around the source lakes area.

Family: Viperidae

Bitis (Bitis) arietans (Merrem, 1820)

Puff Adder (Fig. 34, Map 33)

Material: PEM R23296, Delala River, near Samunanga village, Moxico Province, -12.93169° 18.81458° , 1,363



Fig. 34. *Bitis (Bitis) arietans* from Delala River, near Samunanga village. Photo by Luke Verburgt.

m asl; PEM R23373, en route from Quembo to Cuanavale, Moxico Province, -13.50839° 19.14667° , 1,389 m asl; PEM R23394, Cubango River Source, -12.66068° 16.09468° , 1,763 m asl. **Additional photographic record:** Cuatir, Cuando Cubango Province, -16.48523° 18.20304° , Stefan van Wyk. **Description:** Dorsal scales heavily keeled, in 28–31 rows at midbody; 121–129 smooth ventrals; 23–29 paired subcaudals; 7–9 interorbitals; 3 interoculabials; 13–15 circumorbitals; 13–16 supralabials; 16 infralabials, the first four in contact with the anterior chin shield; cloacal scale entire. Largest female: 309 + 36 mm (PEM R23394); largest male: 631 + 98 mm (PEM R23296). **Habitat and natural history notes:** The specimens from the source lakes area were found in open grassland associated with the drainage lines. **Comment:** This venomous species is common and widespread throughout Angola (Marques et al. 2018).

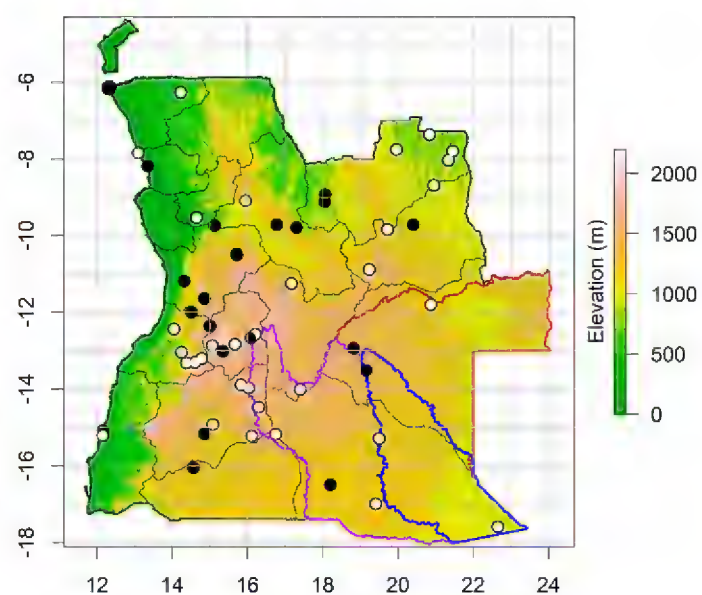
Bitis (Macrocerastes) gabonica (Duméril, Bibron, and Duméril, 1854)

Gaboon Adder (Fig. 35, Map 34)

Material: PEM R23374, near Samunanga village, Moxico Province, -12.89228° 18.8605° , 1,363 m asl; Sight record, road east of Luena, -13.17558° 21.17988° , ~1,146 m asl. **Additional photographic records:**

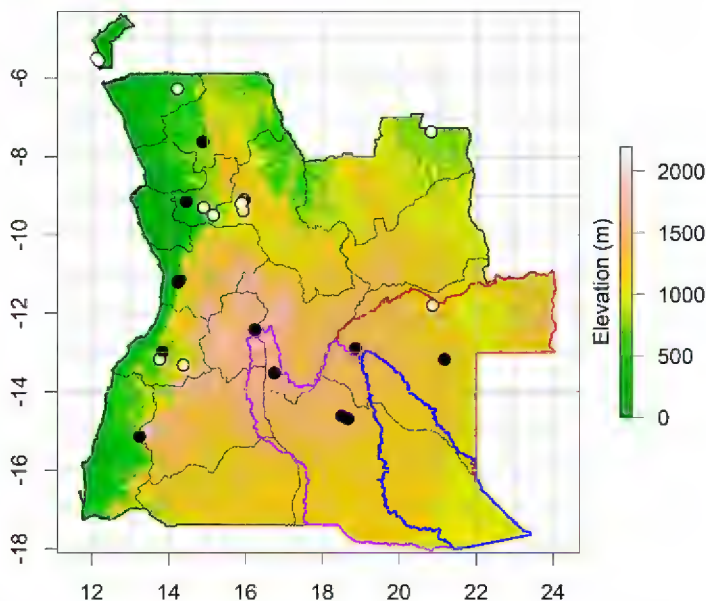


Fig. 35. *Bitis (Macrocerastes) gabonica* from near Samunanga village. Photo by Werner Conradie.



Map 33. Distribution of *Bitis (Bitis) arietans* in Angola.

22 km east of Longa, Cuando Cubango Province, -14.68680° 18.66540° , John Mendelson; 2.8 km south-east of Longa, Cuando Cubango Province, -14.61600° 18.50380° , John Mendelson; Cusseque/Chitembo, Bié Province, -13.51863° 16.75419° , Manfred Finckh. **Description:** Dorsal scales heavily keeled, in 42 rows at midbody; 129 smooth ventrals; 29 paired subcaudals; 13–15 interorbitals; 4 interoculabials; 15 circumorbitals; 15 supralabials; 19 infralabials, the first four in contact with the anterior chin shield; cloacal scale entire. Size male: 1,100 + 135 mm (PEM R23374). **Habitat and natural history notes:** This specimen was caught in a pitfall trap dug by the locals for catching animals in the Angolan Miombo woodland. **Comment:** Previously, this species was mostly known from northern Angola, with some records from Benguela and Moxico provinces (Marques et al. 2018), later being recorded as far south as Caimbambo, Benguela Province (Oliveira et al. 2016) and Tchivinguiro, Huíla Province (Branch, unpub. data). The new records from this study as well as unpublished TM records, virtual museum records (ReptileMap 166065; iNaturalist 33760143, 34126489), and photographic records (J. Mendelsohn) extend the distribution of this species as far south as Longa in Cuando Cubango Province, filling the gap between the northern and southern records. The new material documented from



Map 34. Distribution of *Bitis (Macrocerastes) gabonica* in Angola.



Fig. 36. *Causus bilineatus* from Quembo River source. Photo by Luke Verburgt.

this study is the first for south-eastern Angola and the Okavango Delta system.

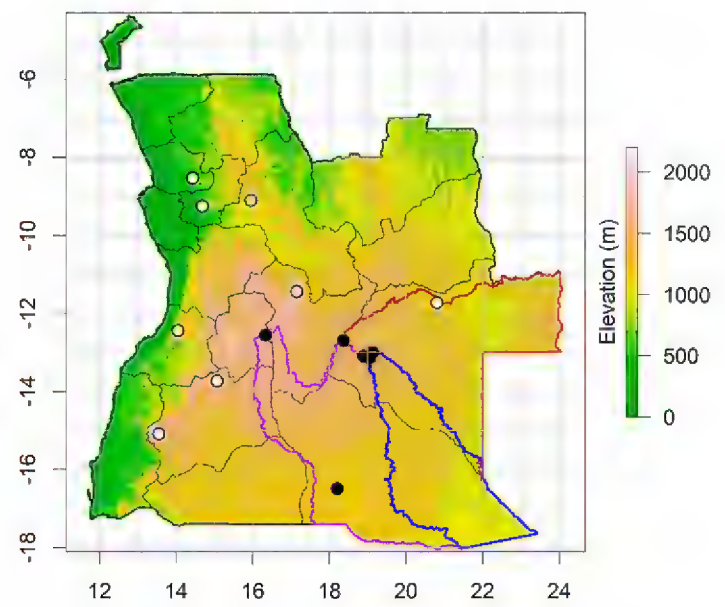
Causus bilineatus Boulenger, 1905

Two-lined Night Adder (Fig. 36, Map 35)

Material: PEM R23268–70, Cuanavale River source lake, Moxico Province, -13.09330° 18.89396°, 1,367 m asl; PEM R23321, Cuito River Source Lake, Moxico Province, -12.68935° 18.36012°, 1,435 m asl; PEM R23428–9, Cuando River Source Trap 2, Moxico Province, -13.00426° 19.12719°, 1,350 m asl; PEM R23437, Cuando River Source Trap 1, Moxico Province, -13.00393° 19.12808°, 1,351 m asl; PEM R23451–2, Quembo trap 4, Moxico Province, -13.13586° 19.04709°, 1,368 m asl; PEM R23464–5, INBAC: WC-4727, Quembo trap 1, Moxico Province, -13.13592° 19.04417°, 1,369 m asl. **Additional photographic record:** Cuatir, Cuando Cubango Province, -16.48523° 18.20304°, Stefan van Wyk. **Description:** Dorsal scales smooth and in 17 rows at midbody; 129–135 smooth ventrals; 24–32 paired subcaudals; 2 preoculars; 2 postoculars; temporals mostly 2+3; 6 supralabials; 9 infralabials, the first four in contact with the anterior chin shield; cloacal scale entire. Largest female: 337 + 38 mm (PEM R23321); largest male 350 + 53 mm (INBAC: WC-4727). **Habitat and natural history notes:** This species



Fig. 37. *Causus rhombeatus* from Quembo River source. Photo by Werner Conradie.



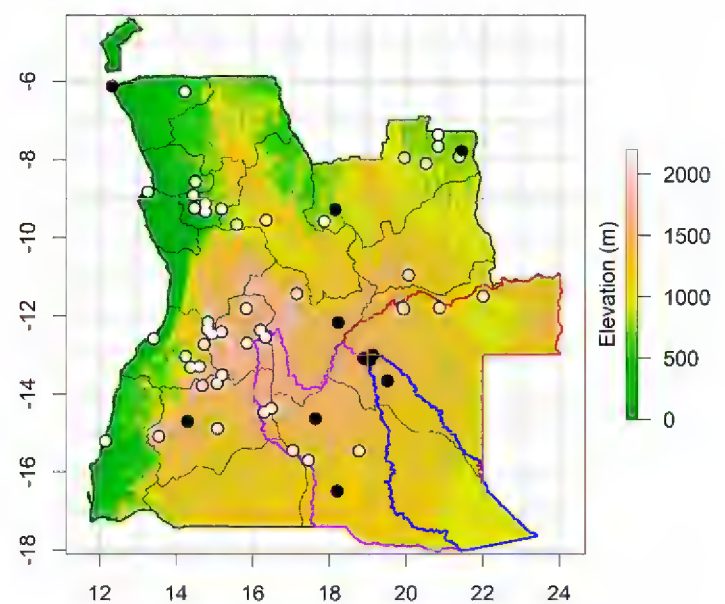
Map 35. Distribution of *Causus bilineatus* in Angola.

is associated with wetlands and rivers. The stomachs of specimens contained various frogs (*Ptychoadena taenioscelis*, *P. uzungwensis*, *Hyperolius nasutus*, and *Breviceps ombelanonga*). One female (PEM R23429) collected in November 2015 had four fully developed eggs, the largest measuring 12.8 x 6.5 mm. **Comment:** This species has mostly been recorded from central and western Angola (Marques et al. 2018) with the only known record from eastern Angola being from Lake Calundo, Moxico Province (Laurent, 1964). Marques et al. (2018) assigned Bogert's (1940) *C. rhombeatus* specimen from Capelongo to *C. bilineatus* following Manaças (1981), however Rasmussen (2005) examined the same material and assigned it to *C. rhombeatus*. The recently collected material is the first from the Okavango Delta system. The southernmost record of this species is from Cuatir, Cuando Cubango Province.

Causus rhombeatus (Lichtenstein, 1823)

Rhombic Night Adder (Fig. 37, Map 36)

Material: PEM R23405, Cuando region, Moxico Province, -13.66494° 19.51381°, 1,277 m asl; PEM R23438, Cuando River Source Trap 1, Moxico Province, -13.00393° 19.12808°, 1,351 m asl; PEM R23488, Quembo trap 2, Moxico Province, -13.13544° 19.04397°, 1,375 m asl; PEM R27358, Cuanavale River source



Map 36. Distribution of *Causus rhombeatus* in Angola.

lake, Moxico Province, -13.09052° 18.89394°, 1,357 m asl; PEM R27359, wetland near old quarry west of Quemba, Bié Province, -12.16960° 18.22965°, 1,353 m asl. **Additional photographic records:** Cuatir, Cuando Cubango Province, -16.48523° 18.20304°, Stefan van Wyk; Menongue, Cuando Cubango Province, -14.63015° 17.63465°, Stefan van Wyk. **Description:** Dorsal scales smooth and in 18–20 rows at midbody; 136–146 smooth ventrals; 26–36 paired subcaudals; 2 preoculars; 2 postoculars; temporals 2+3; 6 supralabials; 9 infralabials, the first four in contact with the anterior chin shield; cloacal scale entire. Largest female: 652 + 82 mm (PEM R23488); largest male 611 + 93 mm (PEM R27358). **Habitat and natural history notes:** One specimen was found preying upon a *Sclerophrys pusilla*. **Comment:** This venomous species is widespread throughout Angola (Marques et al. 2018). Adult material from eastern Angola lacks the distinct dark vertebral black blotches and is more olive in coloration than the southern African material, while juveniles are greyish with distinct black vertebral blotches.

Discussion

This study covers an extensive area in south-eastern Angola that was previously very poorly surveyed. It increases the total number of snake species recorded for the country to 133. At a regional level, the results raise the total number of species known from the Angolan Okavango-Cuando-Zambezi river system to 53 species, an increase of 16 species from a previously compiled checklist for the region (Conradie et al. 2016). This survey confirms the presence of four species previously predicted to occur in the region (*Elapsoidea s. semiannulata*, *Amblyodipsas p. polylepis*, *A. ventrimaculata*, and *Crotaphopeltis barotseensis*, the latter two representing the first country records (Branch 2018)). The first genetically confirmed records of *Dasypeltis confusa* and *Psammophis zambiensis* (Keates 2021; W. Conradie, unpub. data) and the second record of the rarely sighted *Psammophis jallae* for Angola are also documented here.

Material collected in this under-surveyed region led to the description of two new snake species for Angola (Hallermann et al. 2020), contributed substantially to several studies on African snake genera over the last few years (e.g., Portillo et al. 2018, 2019; Engelbrecht et al. 2019, 2020; Keates et al. 2019; Conradie et al. 2020; Deepak et al. 2021), and will certainly be used in further studies. These publications highlight the relevance at both the national and continental levels of such surveys in undersampled regions of Angola, as they not only help document the area and justify its conservation value, but also contribute to the clarification of taxonomic issues and biogeographical patterns at broader scales.

A compilation of all the snake species previously recorded from adjacent Zambia, Namibia, and Botswana

(Auerbach 1987; Branch 1998; Broadley et al. 2003; Broadley and Blaylock 2013) shows that we have recorded at least 10 new species for the Okavango Delta system: *Bitis gabonica*, *Boaedon angolensis*, *B. branchi*, *B. fradei*, *Causus bilineatus*, *Dasypeltis confusa*, *Namibiana rostrata*, *Philothammus heterolepidotus*, *Prosymna angolensis*, and *Psammophis zambiensis*. Additional surveys in south-eastern Angola will likely add more entries to the growing list of species known from the Angolan Okavango-Cuando-Zambezi river drainages, among which the following are expected: *Afrotyphlops mucruso*, *A. schlegelii*, *Atractaspis bibroni*, *Gracililima nyassae*, *Grayia tholloni*, *Hemirhagerrhis nototaenia*, *Hypoptophis wilsoni*, *Limaformosa capensis*, *Psammophis angolensis*, *P. lineatus*, *Psammophylax tritaeniatus*, *Pseudaspis cana*, *Telescopus semiannulatus*, and *Xenocalamus bicolor*.

Updated geographic distribution maps for the whole country of the snake species occurring in south-eastern Angola are presented here, and they include substantially increased numbers of records and distribution ranges for certain species, such as *Bitis gabonica*, *Causus bilineatus*, *Dendroaspis polylepis*, and *Python natalensis*. The results fill large gaps in the geographic distributions of many snake species in central and eastern Angola (see Maps 1–36).

Until recently, south-eastern Angola and its river sources had been relatively protected from human exploitation, mostly due to their remoteness (Mendelsohn and Obeid 2004). After the end of the war in Angola, this scenario started to change gradually (Mendelsohn and Obeid 2004), and the current accessibility of the region is leading to rapid urban growth (Mendelsohn and Weber 2015; NGOWP 2017) and illegal commercial logging, which has escalated during the last few years (Mendelsohn and Martins 2018). The development plans for the region include agriculture, fish farming, and livestock production, among others (Mendelsohn and Martins 2018). All of these developments pose a serious threat to conservation in Angola, and consequently to what lies downstream, including the Okavango Delta (Mendelsohn and Obeid 2004), an UNESCO World Heritage site. Documenting the biodiversity in the region is an essential step in justifying the urgent need for the protection of this unique and vulnerable section of Angola and Africa.

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